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The water-hopping kinematics of the tree-climbing fish, *Periophthalmus variabilis*

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ABSTRACT

In this communication, we describe the water-hopping kinematics of the dusky-gilled mudskipper (*Periophthalmus variabilis*), and by doing so elucidate an entirely new form of fish locomotion that has yet to be reported in the public domain. Water-hopping is defined herein as an ability to hop once, or in succession, on the surface of water without full submergence and without a fin-guided glide. We find that taxiing on the water surface is the predominating kinematic movement used for the execution of successful water-hops. We observe that an initial concentric ripple forms as the mudskipper impacts the water, and that subsequent taxiing on the water surface generates a sinusoid-like ripple pattern in the water prior to take off. Interestingly whilst airborne, the pectoral fins of *P. variabilis* appear to remain stationary, only to be deployed immediately upon contact with the water. When landing back onto the surface of the water, *P. variabilis* makes the initial contact via its pelvic region, occasionally extending its pectoral fins during its descent. The reasons for pectoral and pelvic fin extension are unclear, however, there may be either aerodynamic or hydrodynamic benefits in its doing so. This motion furthermore prepares the mudskipper for either, a follow-on water-hop, or a discontinuation of movement altogether, as the body of the mudskipper becomes aligned in a way conducive to either. *P. variabilis* will launch and land using both, horizontal surfaces such as littorals, and inclined-to-vertical surfaces such as rocks and trees.

Key words: Mudskipper, *Periophthalmus variabilis*, Kinematics, Gobiidae, Water-Hopping

1. INTRODUCTION

A large number of fish species are able to launch into the air from water. These include the common carp (*Cyprinus carpio*; Stuart et al., 2011), the African butterfly fish (*Pantodon buchholzi*; Saidel et al., 2004), salmon (Lauritzen et al., 2005), the Trinidadian guppy (*Poecilia reticulata*; Soares and Bierman, 2013), and flying fish (Exocoetidae), which are also able to glide (Davenport, 1994). A much larger sized aruana (arowana) fish of the Amazon (*Osteoglossum bicirrhosum*) (*ca.* 1 m long and 3 kg weight) (Verba et al., 2018) captures small birds and snakes (e.g. two thread-snakes, Leptotyphlops macrolepis) by launching itself above the water surface (Goulding, 1989). However, to the best of our knowledge, there are no records of fishes hopping repeatedly across the water surface as a means of locomotion. This paper concerns our observations of fish hopping on the water surface (hereinafter: water-hopping) between launches and landings upon trees, mangrove roots, rocks or littorals. Water-hopping, as is reported in this paper, may have developed through a need to evade predatorial attack, or as a migratory push to reach environmentally superior habitats. Killifishes (Cyprinodontiformes) for example, launch themselves from the water onto lily pads to evade predators (Baylis, 1982). The African butterfly fish (*Pantodon buchholzi*) launches vertically from the water (a vertical startle response) to escape predatory attack (Berra, 2001; Saidel et al., 2004). Salmon (genera *Oncorhyncus* and *Salmo*) and rainbow trout (*Oncorhyncus mykiss*) launch themselves from the water during their migration from the sea to rivers to spawn their eggs. According to Lauritzen et al. (2005), the jump that salmons perform to leave lower waters to higher waters (often via a waterfall or rapid), is achieved by an initial accelerated swim, which is then followed by the jump. The jump itself is generated by a spring-like response to the release of stored energy after the fish retracts from a bent body configuration at high speed. Certain fish species remain airborne for relatively long periods of time. One example is the flying fish (Exocoetidae) which has a strong, rigid vertebral column and ossified caudal complexes that allow this fish to stiffen-up while airborne (Dasilao and Yamaoka, 1998). The elongated lower lobe of the fish tail is a primary contributor to power during both taxiing on the water surface and take-off. Taxiing is essentially a behaviour whereby the fish propels itself across the surface of the water, in the case of Exocoetidae, to accelerate for an airborne ascent. The pectoral fins of this fish support its glide, while its pelvic fins behave similarly to the tail-wing of a plane by controlling lift (Davenport, 1994). Speed and body strength during a caudal undulation seem therefore, to be important factors that enable an airborne ascent from water.

A fish may also hop terrestrially by means of a tail-flip, Figure 1. Tail-flips have been observed in small teleost fishes including mosquitofish (*Gambusia affinis*, Cyprinodontiformes) and zebrafish (*Danio rerio*, Cypriniformes). The tail-flip is essentially a fast movement resulting in an extreme curvature of the body with the head bending towards the tail. The centre of mass then transfers to the tail, which is in contact with the ground, and the fish manages to hop (the tail-flip). There are nevertheless variations of this fundamental tail-flip movement that can be observed in other fishes. Quasi-terrestrial blennies (Blennidae) and tidepool gobies (Gobiidae) hop using a laterally-oriented axial bend where the tail (resting on its ventral surface) is flexed towards the head and presses the caudal peduncle towards the substrate for launch (Gibb et al., 2011). Mudskippers have adapted tail movements that form a J-shape, a prone jump (Swanson and Gibb, 2004), when escaping in a terrestrial environment. During a prone jump, a mudskipper bends its tail towards its body, lifts its head slightly at an angle off the ground in preparation for a terrestrial launch (take-off). Its tail rotates before the jump becoming parallel with the substrate, and thus allowing it to push against the substrate for the jump. The mudskipper take-off is reported to be different to that of blennies and tidepool gobies, in that the mudskipper retains ventral contact with the ground during this initial bend, rather than the lateral contact as observed in blennies and tidepool gobies. Moreover, unlike blennies and tidepool gobies, the mudskipper uses both its pectoral fins and pelvic fins to stabilise itself (Gibb et al., 2011). The mudskipper prone jump take-off is finally achieved through the rapid unfolding of its body, which includes a lateral-ventral straightening of its tail coupled to a lift of its centre of mass off the ground, which in combination launches its body into the air. The take-off angle of the mudskipper during a prone jump is reported to vary between 27° and 59° (Swanson and Gibb, 2004).

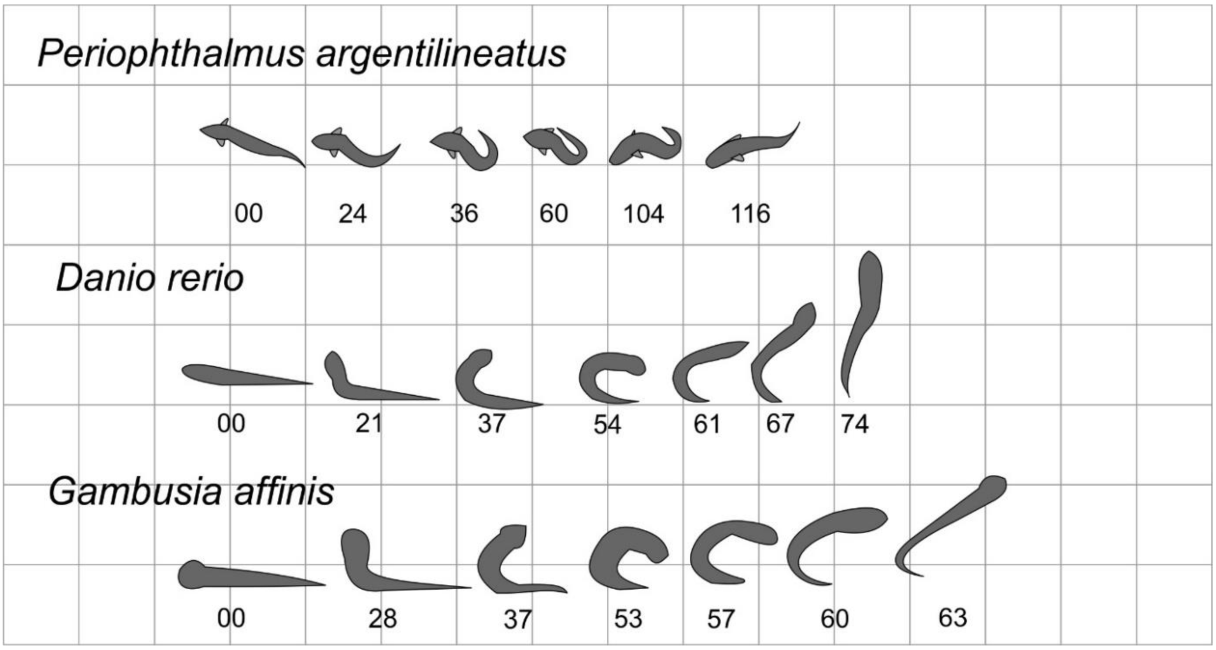

Figure 1. Dorsal view (with its ventral surface on the substrate) of the locomotive behaviour of *Periophthalmus argentilineatus* on solid substrates. Dorsal views of *Danio rerio* and *Gambusia affinis* (with their lateral surfaces on the solid substrate) show these fishes ascend into the air to move across a solid substrate. Numbers indicate sequence of time (in ms). Figure inspired by the works of Swanson and Gibb (2004) and Gibb et al. (2011).

Mudskippers are amphibious fishes that have developed a locomotor ability on land, by which means conduct continuous movements known as 'crutching' (Pace and Gibb, 2009). To improve their locomotive abilities on land, they use their pectoral fins antagonistically with their pelvic fins, such that their pelvic fins are deployed as their pectoral fins are pulled back towards the body, and *vice versa* (Wicaksono et al., 2017). In some cases, mudskippers, such as *Periophthalmus variabilis* have adapted fin-morphologies enabling them to climb on inclined surfaces, vertical trees trunks and igneous rock faces (Wicaksono et al., 2016). Prone jumps, crutching and tree-climbing (a specialised form of crutching), are essentially fully terrestrial behaviours. Besides these terrestrial behaviours, we have recently observed that *P. variabilis* also has a curious part-aquatic, part-terrestrial behaviour, whereby it hops rapidly across the surface of water (water-hopping) between different terrestrial locations. Water-hopping, is a rare kinematic behaviour observed in only a few animals such as skittering frogs (*Euphlyctis cyanophlyctis, Euphlyctis hexadactylus*) (Gans, 1976; Nauwelaerts et al., 2004). This behaviour has not yet been reported as being a kinematic characteristic of mudskippers, or indeed any fish. This paper provides, to the best of our knowledge, the first record of the water-hopping kinematics of mudskippers.

2. MATERIALS AND METHODS

2.1 Filming and video editing

Mudskippers (*Periophthalmus variabilis*) were observed during the month of June between 10 am and 2 pm at their natural habitats in the Mangkang region, Western Semarang, Central Java, Indonesia. The recorded temperature ranged between 31 - 33 °C and relative humidity ranged between 48 - 51%. The act of water-hopping in *P. variabilis* was filmed following gentle encouragement using a tree branch with which we approached the fish from a terrestrial starting point. The terrestrial start-points included littoral zones, the sides of tree trunks, mangrove roots, rock faces and on some occasions, man-made objects such as wooden piles. The entire water-hopping sequences (for kinetic and kinematic analyses were filmed using a GoPro Hero 7 Black (240 fps, 960-pixel, HEVC video setting). The hopping distances were measured by image analysis (ImageJ) of still frames from the video footage, using the actual length of the fish (measured after capture) as a distance scale. Other footage taken using a lower frame-rate camera was not used for calculations within this study but provide useful supplemental video footage. Throughout the length of the hopping sequences, the camera was kept in a flexible handheld tripod to make it easier to follow the fish movements. Filming was conducted in both the plan-view (at *ca.* 50 cm above the fish) and in the lateral view from a distance of *ca.* 10 cm. To reduce measurement errors from out-of-plane fish motion, we rescale every image frame against the measured fish length and interpolate between the measured lengths from consecutive frames. Fish were captured after the filming and their total body lengths (from the tip of the snout to the tip of caudal fin) and weights recorded. Both Adobe Premiere CS5 and VideoPad Video Editor were used to postprocess the video footage, including the different patterns of movement during water-hopping, and the times taken for each hop. Photographs were also taken from the plan (dorsal) and lateral (side) views as an additional aid to capturing the kinematics of motion using a Canon EOS 550D. Photos were taken using the burst mode to ensure that a continuous sequence of images was captured for each individual hopping event.

2.2 Fish length and weight measurements

Mudskippers were captured using a net after which they were transferred to an aquarium with small volumes of water (to prevent damage to the fish exterior through drying and friction). The collected fishes were rinsed from mud using seawater from their original habitats. Neither anaesthesia nor euthanasia were necessary. All fishes were released back into their original habitats after measurements and weights were taken. We followed the National Research Council (2010) protocol: On Handling Fish and Amphibians protocol.

2.3 Kinetics calculations

The mudskipper researched in this work repeatedly contacts the water to take-off most commonly by taxiing on the water surface, which generates kinetic energy and produces the acceleration needed for a subsequent hop. By following the consecutive water-hops of *P. variabilis*, we can better understand how prolonged hopping can affect the airborne kinematics, the energy lost by contacting water, and the impact forces of the fish against water (assuming no compliance for the initial impact).

The kinetic energy during both airborne and water-contact stages is expressed as a function of distance, *d*, travelled, $K_e(d)$ [J/m], Equation 1. In this equation, *m* is the mass of the mudskipper and *v* is its velocity.

$$K_e(d) = \frac{1}{2}mv^2 \cdot d^{-1} \qquad (1)$$

The loss in kinetic energy, K_{e_LOSS} [dimensionless], Equation 2, through contact with water is calculated as the kinetic energy as a function of distance during an airborne stage, $K_{\_e\_AIR}(d)$, divided by the kinetic energy as a function of distance during the following water-contact period, $K_{\_e\_WATER}(d)$. If $K_{e\_LOSS} = 1$, there is no energy lost during a water-contact period directly following an airborne period. Ratios of $K_{e\_LOSS} > 1$ indicate that energy is lost during a water-contact period directly following an airborne period. The higher the value of K_{e_LOSS}, the greater the energy lost. Values of $K_{e\_LOSS} < 1$ indicate that energy is gained during a water-contact period directly following an airborne period.

$$K_{e\_LOSS} = \frac{K_{e\_AIR}(d)}{K_{e\_WATER}(d)} \qquad (2)$$

The impulse, *J* [N·s], is calculated according to Equation 3, and is the momentum of airborne flight (*mv*) less the momentum during a water-contact period (*mu*).

$$J = (mv - mu) \qquad (3)$$

The acceleration or deceleration from a water-air transition (Equation 4) or air-water transition (Equation 5) is simply calculated as the differences in velocity with respect to time. A positive value of either A_{WA} or A_{AW} indicates that the fish decelerates, while a negative value indicates the fish is accelerating.

$$A_{WA} = (v_{AIR} - v_{WATER})/0.5t_{WATER} \qquad (4)$$

$$A_{AW} = (v_{WATER} - v_{AIR})/0.5t_{AIR} \qquad (5)$$

3. RESULTS

During our daylight observations of *P. variabilis* water-hopping, we noted that these mudskippers would generally avoid complete submergence into water, even if being chased. We did note nevertheless, a few instances where mudskippers would enter their burrows after hopping events. From our observations, we note that the mudskippers appeared to use water-hopping as a means coming closer to their burrows when threatened. In the vast majority of water-hopping events, mudskippers would begin on a solid substrate and end on a solid substrate, hopping upon the water surface in between. The solid substrates could be at any inclination (i.e. from horizontal to vertical) and mudskippers were observed launching from and landing on tree trunks, mangrove roots, littorals, rock faces and man-made structures such as wooden piles. The generic method of water-hopping involved an initial launch from a stationary solid substrate into an airborne ascent. After this, the mudskipper would descend and make contact with the water surface, after which it would water-hop to ascend from the water surface into the air once again. This water-hopping behaviour could continue for either shorter (3 hop) or longer (5 hop) sequences and would end when the fish water-hopped from the water surface back to a solid substrate. In the following sections, we shall describe the different stages of water-hopping in greater detail.

3.1 Water-hopping: periods in contact with the water surface

Figure 2 shows schematics of generic water-hopping events, starting and ending on a solid surface. There were two different water-hopping techniques observed for the periods spent on the water surface. The first and more common of the two, involved taxiing on the water surface (Supplementary Video S1) prior to an airborne ascent (Fig. 2A1 plan view, and A2 side view). In the second (more rarely observed) technique, the fish simply bounced (Supplementary Video S2) off the surface of the water into an airborne ascent without any taxiing on the water surface (Fig. 2B1 plan view, and B2 side view). Taxiing refers to a process of movement across the water surface, which we note is most commonly used to build up the speed needed to for an airborne ascent. Upon contact with the water, *P. variabilis* taxis by cyclically undulating its tail (caudal fin and caudal end of the body) from side to side (i.e. laterally) in similitude to the taxiing behaviour of the flying fish (Exocoetidae) (Franzisket, 1965 *cit.* Davenport, 1994), albeit for shorter periods of time than the flying fish. *P. variabilis* conducts a taxi rapidly on the water surface to enable sufficient acceleration for an airborne ascent (as depicted in Figs. A1 and B1 (plan view) and Figs. A2 and B2 (lateral view)).

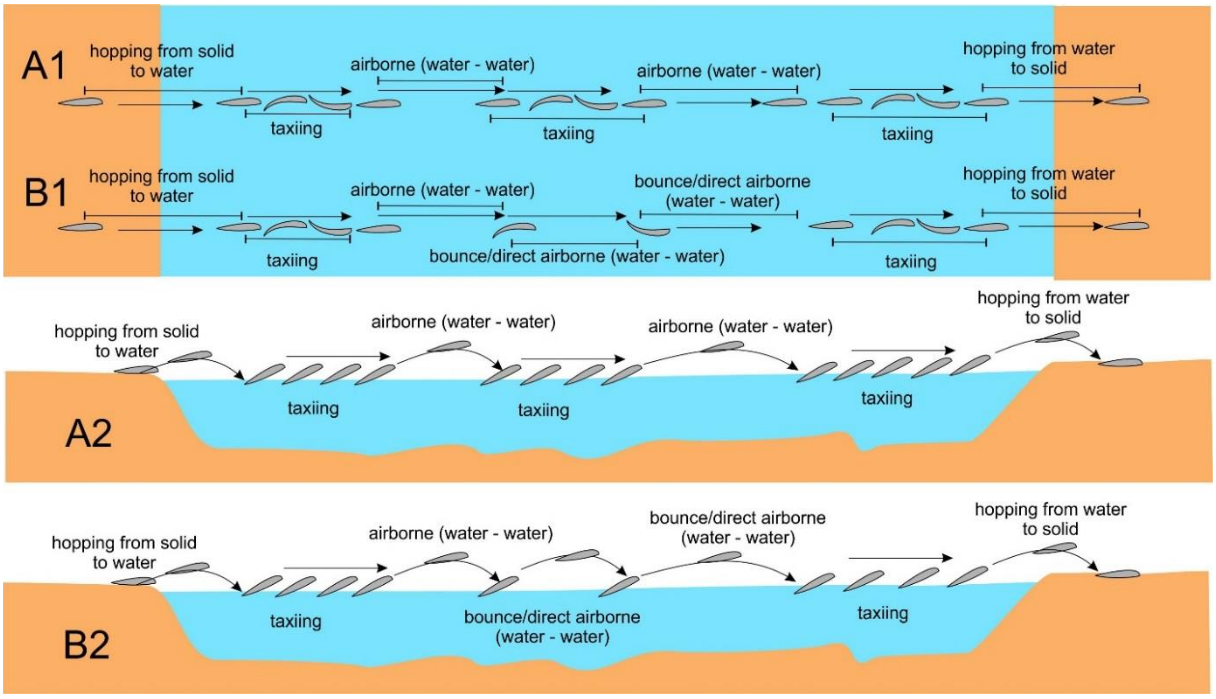

Figure 2. Schematics of the two different water-hopping techniques used by *P. variabilis* for periods spent in contact with the water-surface. In A1 (plan) and A2 (lateral), the mudskipper hops from a solid substrate and then taxis to accelerate into an airborne hop. On landing, it taxis again before an airborne ascent. In B1 (plan) and B2 (lateral) the fish has a sufficiently high kinetic energy coupled to a favourable angle of incidence to allow it to bounce off the water into an airborne ascent (without taxiing on the water-surface).

On observing the wake patterns that develop on the water surface for the more common of the two techniques described above, we find that water-hopping results in two distinctly separate zones of ripple formation, Figure 3 (Supplemental Video S3). The first zone has an undulating ripple pattern (Fig. 3, green lines), which is a consequence of taxiing prior to take off, involving rapid movements of the caudal part of its body and tail. The second zone (Fig. 3, black lines) sees an emerging concentric ripple pattern, which is an aftershock ripple caused by the initial impact of the mudskipper on the water surface. During a water 'bounce' technique as described above (i.e. no taxiing), we only observe these concentric ripples (in black) caused by mudskipper impaction with the water.

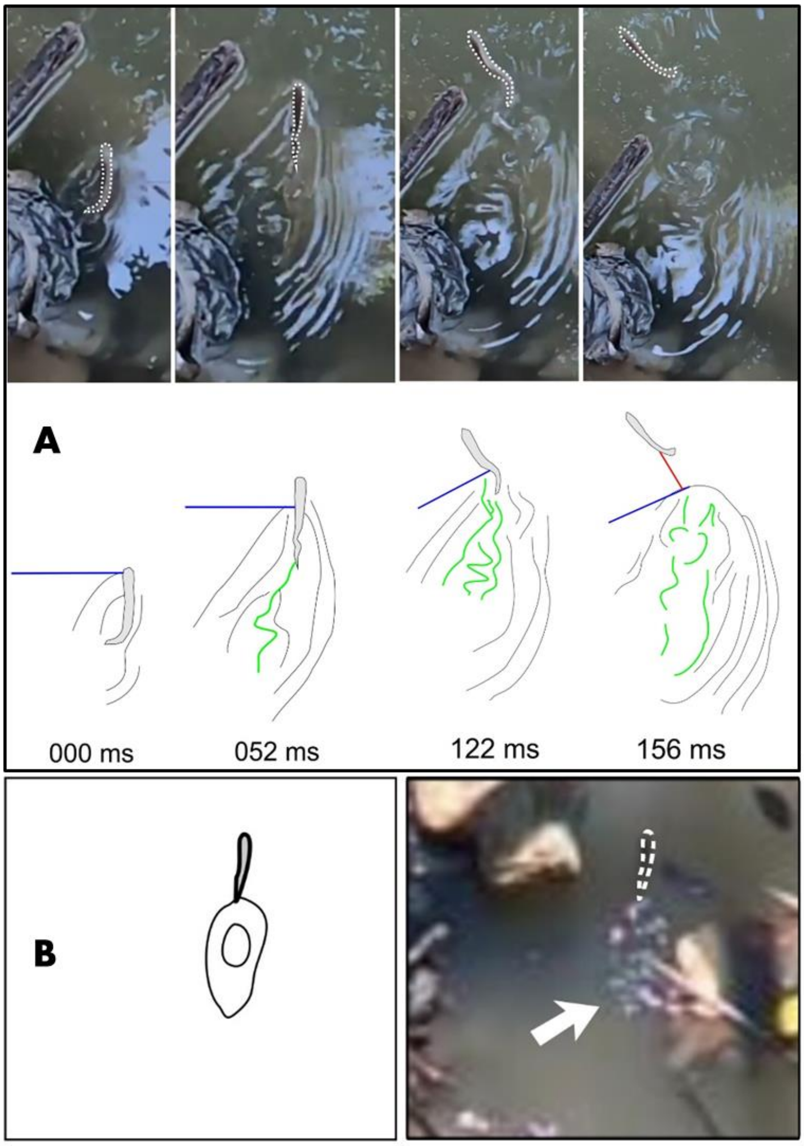

Figure 3. (A). Video stills and accompanying qualitative schematics of ripple patterns generated by *P. variabilis* (outlined by white dots in the video stills) during a water-hop for the period that the mudskipper impacts and taxis on the water surface. Blue lines in the schematics indicate the final position of body contact with the water surface (body parts posterior to this line are still in contact with the water). The maroon coloured line indicates the distance of the mudskipper's body from the water after its airborne ascent. Green lines indicate the ripples that result from taxiing, which is used to accelerate to an airborne ascent. Black lines show the concentric ripples that form after initial impact with the water surface. (B). For a water-bounce

(i.e. no taxiing), only these black concentric lines are observed (schematic on left placed image in B is taken from the video still on the right placed image in B).

3.2 Water-hopping: airborne periods and landing

A build up to a taxi followed by an airborne ascent is shown in Figures 4 (also *cf.* Figure 2). In this figure, the body angles are depicted using dots and lines under each still frame. After hopping from a solid substrate, or, following a previous hop, the mudskipper bends its caudal segment into a small J-shape (0 - 27 ms). After this, the body bends caudally into a J-shape (27 - 36 ms), after which the J-bend undulates toward its caudal fin, pushing the water behind it using a strong stroke of its tail (63 – 72 ms).

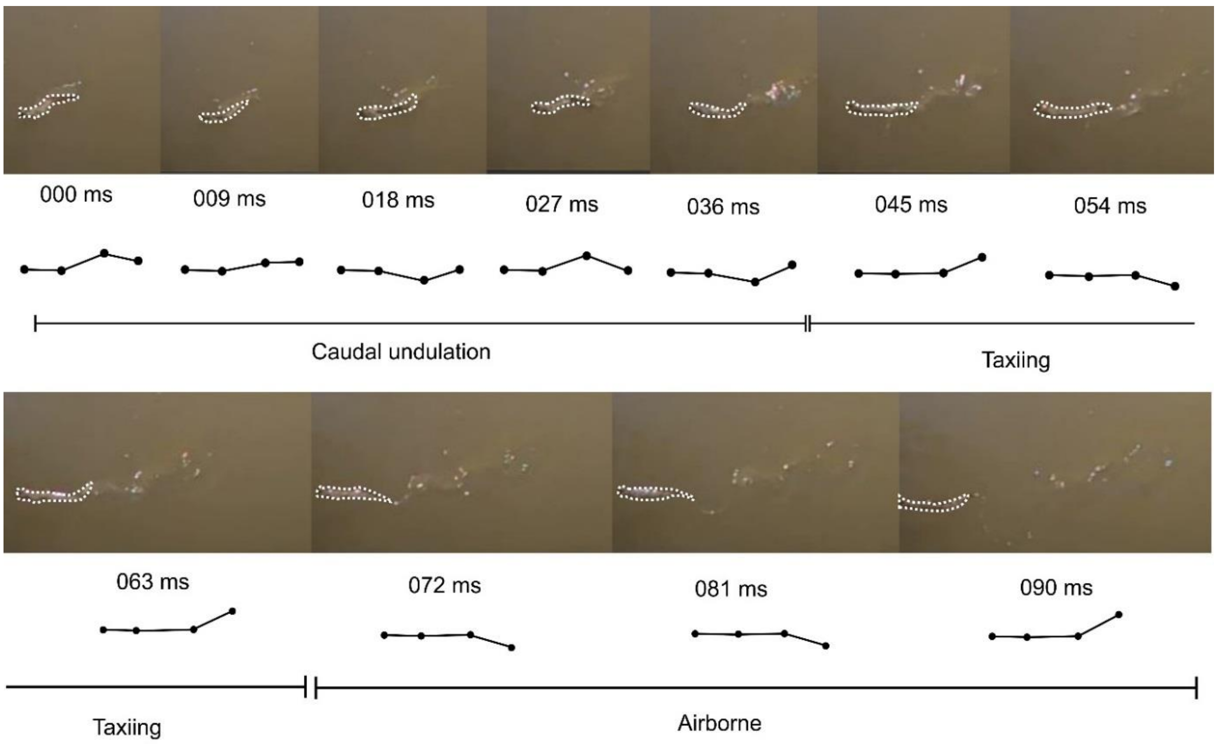

Figure 4. Caudal body postures during taxiing into an airborne ascent. The black dot-line figures indicate the body shape in each still frame and line segmentation is based on the more prominent bends observed along the length of the body in each of the still images. The mudskipper's head is on the left (first black dot on left) and the tip of the caudal is on the right (first black dot on right). The mudskipper is outlined with white dots for clarity in the still images.

When landing either onto a solid substrate or onto the surface of the water, we noted that there were a few instances where the pectoral fins were extended Figures 5 - 6. Fig. 5(A) provides a scheme of the relative positions of pectoral and pelvic fins on *P. variabilis*. In Fig. 5 (B1) we note the pectoral fins are extended after *P. variabilis* hops onto a tree and in Fig. 5 (B2) the pectoral fins are observed as extended when landing onto a littoral. It also appears that the mudskipper occasionally extends its pectoral fins when landing back onto the surface of the water (Fig. 5 (C - E); Fig. 6 (A - B); Supplementary Video S1).

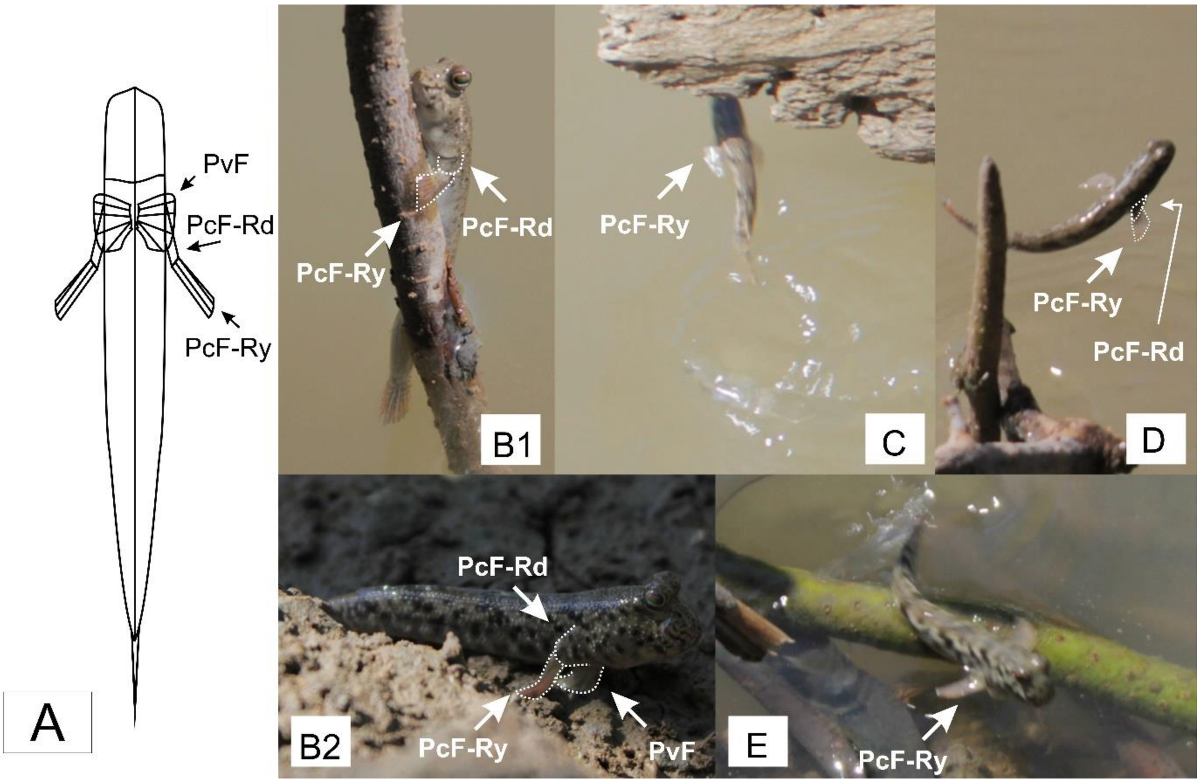

Figure 5. (A) Schematic of the underside of *P. variabilis*, specifically highlighting (black arrows) the pectoral fin radial (PcF-Rd), the pectoral fin ray (PcF-Ry; not spread/extended), and the pelvic fin (PvF), all as seen from a ventral perspective. (B1) A photographic lateral view of *P. variabilis* grabbing onto a root and (B2) perching on land. (C - E) *P. variabilis* water-hopping with extended pectoral fins (dorsal view C, D & dorso-lateral view E). Some fin parts are outlined with white dots for greater clarity.

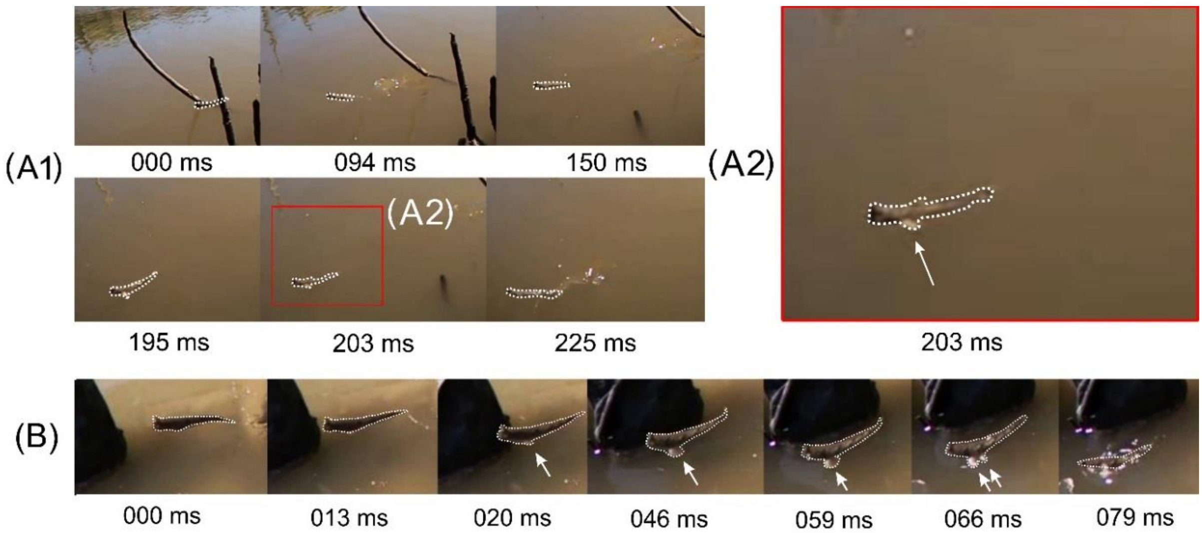

Figure 6. Examples of pectoral fin extensions (white arrow) prior to landing on the water (A1 and B) – see also Supplementary Video S1. Note: In (A1) the red box within the still frame at 203 ms is enlarged on the right hand side of the figure (A2) for clarity.

3.3 Body postures during a generic water-hopping sequence

The body postures through each of the stages of water-hopping are shown in Figure 7. The pectoral and pelvic fins are typically extended when the fish is at rest on land (Fig. 7A). As the mudskipper hops from the land towards the water surface, it bends its tail laterally into a prone jump posture (J-start), subsequently thrusting it rapidly back into position, with a ventral lean, thereby initiating its airborne ascent (Fig. 7B). While in the air, the pectoral and pelvic fins retract to the body (Fig. 7B3, C1), just before the fish lands back onto either the water surface or a solid substrate, it deploys its pectoral fins (Fig. 7C2). After landing onto water, the body then contacts the water surface pelvis first (on its ventral surface) in a straight-bodied position, after which the fish bends the caudal part of its body (Fig. 7D1). Following the caudal bend, the fish starts to taxi to generate thrust for an airborne ascent, this time from the water surface. The fish is also able to redirect its motion from the water-hop by bending its head to a new direction whilst simultaneously bending its tail into a subsequent propulsive thrust from taxiing (Fig. 7D2). This ability to switch directions while water-hopping, will be detailed further in Section 3.5.

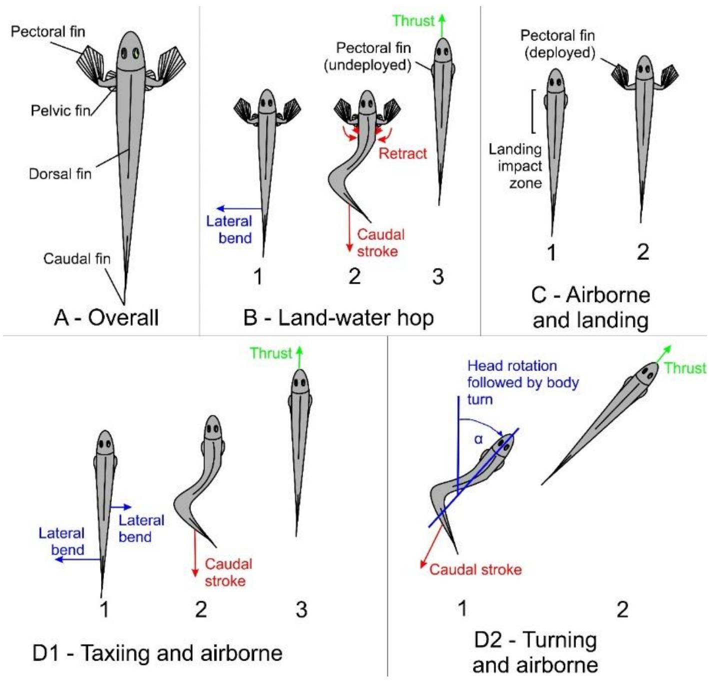

Figure 7. Detailed illustration of *P. variabilis* postures during water-hopping (as illustrated in Figure 2). (A) depicts the mudskipper with both pectoral and pelvic fins fully extended while resting on a solid substrate (e.g. tree face or littoral zone). To hop from land onto the water surface (B), the mudskipper shifts it tail sideways (B1, tail movement indicated by the blue arrow) posturing for a prone jump (J-start), after which it rapidly extends its tail (caudal direction) while retracting its pectoral and pelvic fins (B2, direction of tail and fin movements shown by the red arrows) resulting in the mudskipper launching into the air (B3, airborne thrust force shown in green arrow). While airborne, the mudskipper prepares itself for a landing onto its pelvic region (C1) and before reaching the land/water surface, it deploys both of its pectoral fins (C2). As it lands onto the water surface (or sometimes just before), the mudskipper retracts its pectoral fins and start to taxi on the water surface (D1-1, caudal undulations indicated by the blue arrows leading into D1-2). The final thrust from taxiing involves a strong caudal stroke to launch the mudskipper from the water surface into the air (D1-3, airborne thrust force shown in green arrow). Occasionally, the mudskipper changes direction on the water surface while taxiing by initially bending its head. The rest of the body (D2-1) follows as it completes its final thrust from taxiing, launching itself from the water surface into the air once again (D2-2, airborne thrust force shown in green arrow).

3.4 The kinetics of generic water-hopping events

Mudskipper water-hopping events exhibited notable variations in terms of the velocities, distances, and durations measured. There were also variations noticed between different periods of a water-hopping event. These differences are shown for different individuals (some individuals being observed and recorded on more than one occasion) in Table 1, averages and standard deviations are provided in this table.

Table 1. Average values recorded for different stages of a water-hopping event including airborne periods (after taxiing), airborne periods from a water-bounce, hops to the water from a solid substrate, hops to a solid substrate from the water, and the periods of taxiing. Standard deviations are provided in parentheses. Videos were recorded at 240 fps. Information on the number of times each fish was recorded for each behaviour is provided in the Electronic Supplemental Material SM1.

Behaviour	Number of fish filmed	Total No. recorded hops	Distance travelled (cm)	Duration (ms)	Velocity (m/s)
Hopping from solid substrate to water	14	30	11.3 (± 6.8)	158.8 (± 143.1)	0.9 (± 0.6)
Taxiing	16	52	10.7 (± 5.2)	106.1 (± 77)	1.2 (± 0.7)
Airborne (after taxiing)	19	60	20.6 (± 7.4)	126.9 (± 46)	1.7 (± 0.5)
Water bounce (no taxiing)	7	11	3.5 (± 0.7)	79 (± 43.6)	0.6 (± 0.2)
Airborne (after bounce)	7	11	19.8 (± 6.5)	174.5 (± 59.3)	1.2 (± 0.5)
Hopping to solid substrate from water	18	21	13.7 (± 7.8)	149.5 (± 85)	1.17 (± 1.0)

As can be seen in Table 1, when water-hopping, the highest calculated velocities, 1.7 ± 0.5 m/s occur when the fish is airborne, and most notably after taxiing. The taxiing itself is slightly lower in velocity (1.2 ± 0.7 m/s), however it is interesting to note that taxiing results in a higher velocity than the water contact period of a bounce, which is on average the slowest (0.6 ± 0.2 m/s) of all the water-hopping behaviours in this table. The average airborne hopping velocity that originates from a water-bounce is twice as high (1.2 ± 0.5 m/s) as the bounce upon the water. Hopping from a solid substrate onto the water surface is the second slowest of all the water-hopping stages (0.9 ± 0.6 m/s) and is the only stage that does not benefit from the momentum of a previous kinetic stage. Importantly, we find that *P. variabilis* does on average appear to slow down when hopping from water to land (1.17 ± 1.0 m/s). Nevertheless, the high standard deviation negates any firm conclusions that can be made in this regard.

$K_e(d)$ values are plotted as histograms for short water-hopping sequences, longer water-hopping sequences, and water bounces, Figure 8 (*cf.* Figure 2). The average mass of 8 mudskippers captured by net was recorded as 1.375 g (SD ± 0.276 g). $K_e(d)$ in the short hop sequence (Fig. 8A, left) can be seen to increase over each consecutive airborne and taxiing period, which indicates that the most powerful hops occur after taxiing, and generate greater momentum for a subsequent airborne ascent. However, during longer sequences of water-hops (Fig. 8A, middle), $K_e(d)$ is seemingly more random, increasing and decreasing without any observable pattern. This is also evident in the cases where the fish bounces on the water surface without taxiing, (Fig. 8A, right).

When considering K_{e_LOSS} (energy lost), we note in the short water-hopping sequence Fig. 8 (B, left) that we can see energy is lost from air to water between consecutive jumps, with the first hop losing more energy than the second. In both, the longer hopping sequences (Fig. 8 B, middle) and the bounces, Figure 8 (B, right), the majority of cases see a loss in energy when the fish contacts the water. Generally, water bounces result in the lowest energy losses from airborne to water-contact periods. This is most likely to be because the fish, when bouncing, experiences less hydrodynamic drag than when taxiing, as it spends less time on the water surface.

Results for impulse (J) are shown in Figure 8 (C) and we note that in the cases of short water-hopping, Figure 8 (C, left), and water bouncing, Figure 8 (C, right), sequences, there is a gradual decrease in the momentum lost from the first to the last water-hop. The longer water-hopping sequences, Figure 8 (C, middle), show greater randomness in the impulse values for each consecutive water-hop.

Air-to-water and water-to-air accelerations and decelerations are shown in Fig. 8 (D). Importantly, we note that in all cases, the fishes accelerate during water-air transitions, while they decelerate during air-water transitions. The deceleration from air-water transitions is due to the hydrodynamic drag forces working against the mudskipper in motion, which are considerably more detrimental than aerodynamic drag forces. The acceleration from water to air is a result of the fish taxiing in both long and short sequences of the more commonly observed taxiing water-hop. However, in the cases of water water-bounce, we postulate that this may be due to the immediate switch from a hydrodynamic to aerodynamic environment, which reduces the effect of drag forces on the fish.

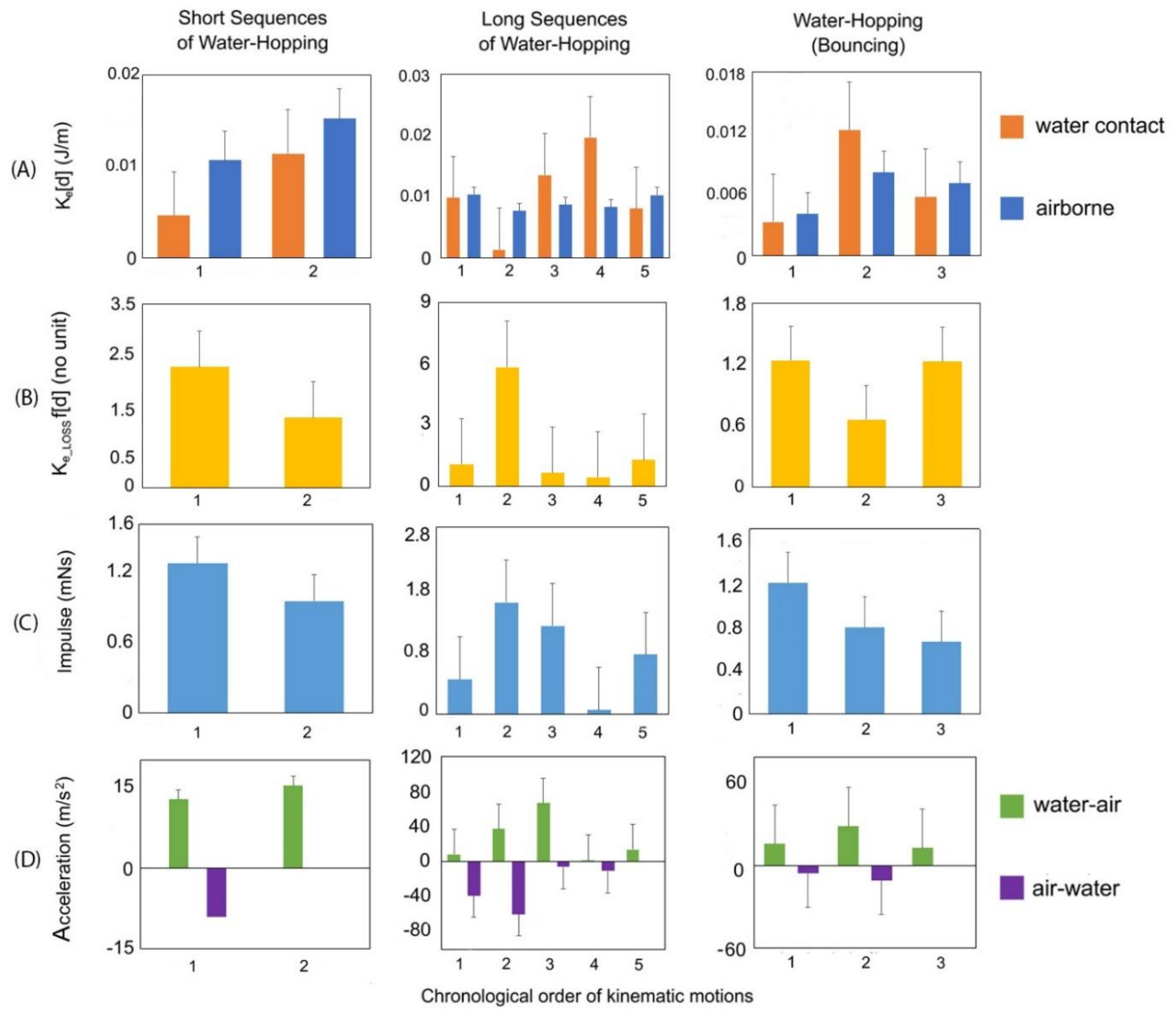

Figure 8. Histogram showing the kinetics of water-hopping mudskippers as measured over a shorter period of water-hops (n = 8), longer period of water-hops (n = 4) and from water-bounces (n = 2). (A) Kinetic energy as a function of distance plotted against each water-hop (split into airborne and taxiing/bouncing periods – *cf.* Figure 2) shown in chronological order. (B) Kinetic energy gained as a function of distance plotted against taxiing or bouncing periods during water-hops and shown in chronological order. (C) Impulse of each water-hop where the transition is from an airborne period to a taxiing/bouncing period, and (D) the acceleration of the fish from water-to-airborne stages (green bars) adjacent to its subsequent deceleration (negative acceleration) from airborne-to-water stages (purple bars). Standard deviations are shown using y-error bars.

3.5 Less frequently observed behaviours and their kinetics

While filming, we noted a few less frequently observed behaviours (Figs. 9 - 16). The prone jump for example, enables terrestrial locomotion, as the mudskipper is able to hop on land (Figs. 9A1; 16B). The mudskipper was also occasionally seen to enter the body of water by sliding in under its own body weight (Figs. 9A2; 16E). If the mudskipper was already on an incline (e.g. near vertical on the surface of a tree or mangrove root), it would hop directly from a vertical or inclined position to the water and commence water-hopping therefrom (Figs 9B1; 15; 16H), returning to either an inclined, vertical/near-vertical (c.f. Supplemental Video S8) or horizontal solid substrate (Figs. 9B2; 16G). Sliding on the water surface (Figs. 9C1; 16C) was also observed prior to taxiing, and we occasionally noted that *P. variabilis* would slide to a littoral (Figs. 9C2; 16E). On a few occasions after already performing a number of consecutive water-hops, we noticed that *P. variabilis* would stop hopping and either opt to swim at the water surface (Figs. 9A3; 11; 16F; Supplemental Videos S4 and S5) or, dive under water, possibly to a solid substrate, or to a nearby burrow (Figs. 9A4; 12; 16A; Supplemental Videos S4 and S5).

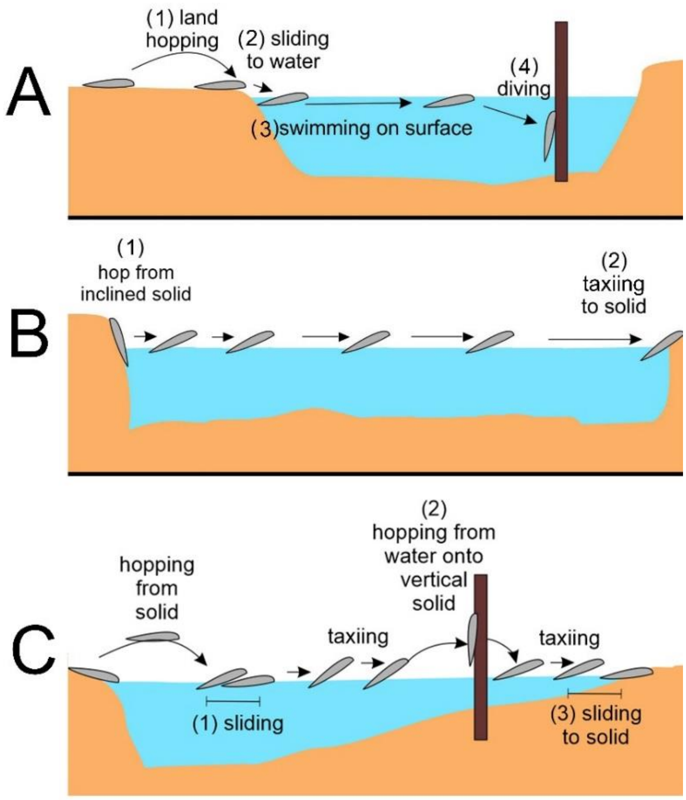

Figure 9. Illustration of less commonly observed behaviours of P. variabilis. (A1) Hopping on a solid substrate (A2) sliding from the ground into the water (A3) swimming on the water surface (A4) diving to a solid substrate (rarely observed) (B1) taxiing directly off an inclined (vertical or near-vertical) surface into the water (B2) taxiing from the water onto an inclined solid (C1) sliding on the water surface before taxiing prior to an airborne ascent (C2) landing on a vertical solid surface from a water-hop (c.f. Supplemental Video S8) and (C3) sliding to the land after landing on the water surface following a water-hop.

From our field observations, we noted that *P. variabilis* displays two general escape trajectories that directly involve water-hopping between areas of land, Figure 10. The path angle (θ) is the angle relative to the original direction of travel. When escaping, the path angle typically lies between 0° and 100°, sometimes retaining a continuous path closer to 0° (near-linear escape), Figure 10A, and sometimes turning sharply on the water at an angle closer to 90° (non-linear escape), Figure 10B (Fig. 13; see also Supplemental Video S6). The non-linear escape involves a sharp turn on the water surface, following which the mudskipper starts water-hopping in the direction to which it turns. The path typically follows a bend of some form with a distinguishable angle of turn, which we observed was often close to 90°. Occasionally, the fish made a U-turn using a short taxi to return to the same littoral from where it left, Figure 10C, see also Fig. 14 and Supplemental Video S7. Table 2 provides kinetic details on these alternative, less often observed behaviours described in this section (3.5), while Fig. 16 provides plan-view kinematic sketches of each behaviour mentioned in Table 2, based on our video footage.

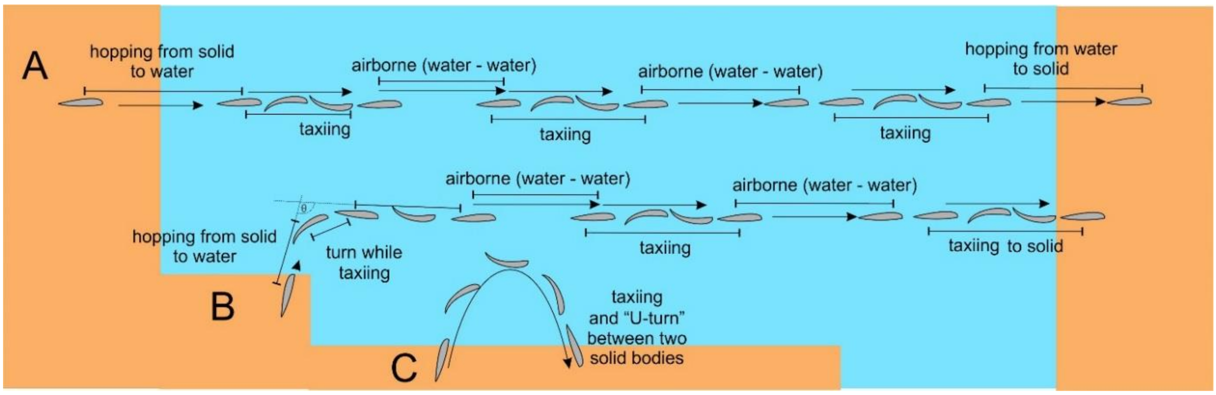

Figure 10. Illustration of (A) normal water-hopping in water as in Fig. 2, (B) water-hopping with an angular turn (Supplementary Video S6), and (C) a U-turn followed by a short taxi to return to the same littoral (Supplementary Video S7).

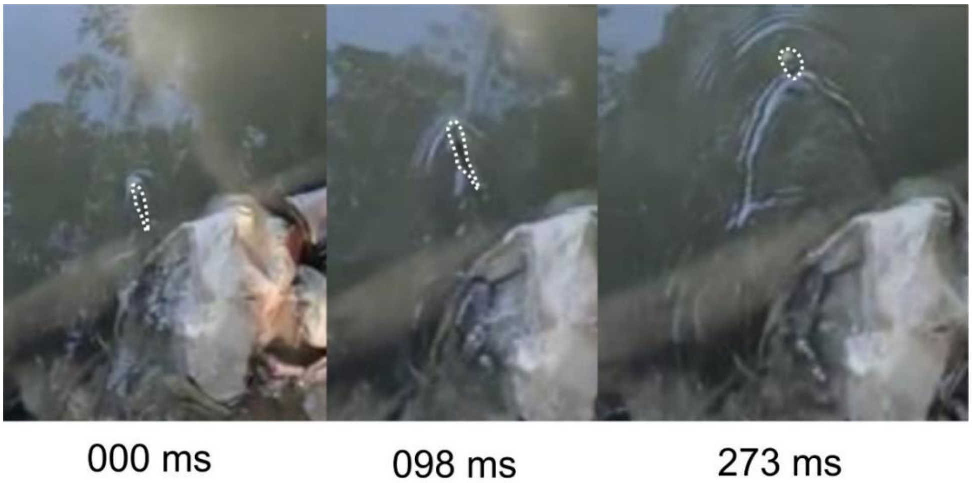

Figure 11. *P. variabilis* swimming on the water surface (Supplemental Video S4). This was a very rarely observed behaviour. The mudskipper employs carangiform type swimming whereby lateral caudal fin undulations occur cyclically to propel the fish forwards. The white dots indicate the parts of the body that are above water.

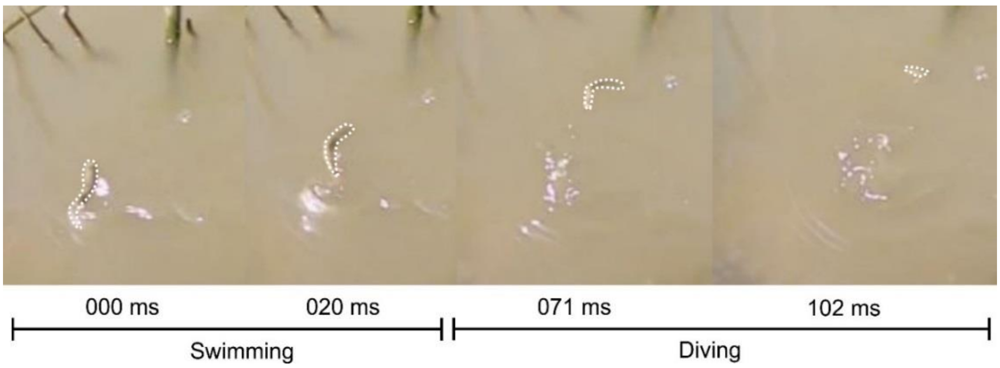

Figure 12. *P. variabilis* diving after it swims on the water surface (Supplemental Video S5), the least frequently observed behaviour. The mudskipper tilts its head to pitch down below the water surface. The mudskipper is outlined with white dots.

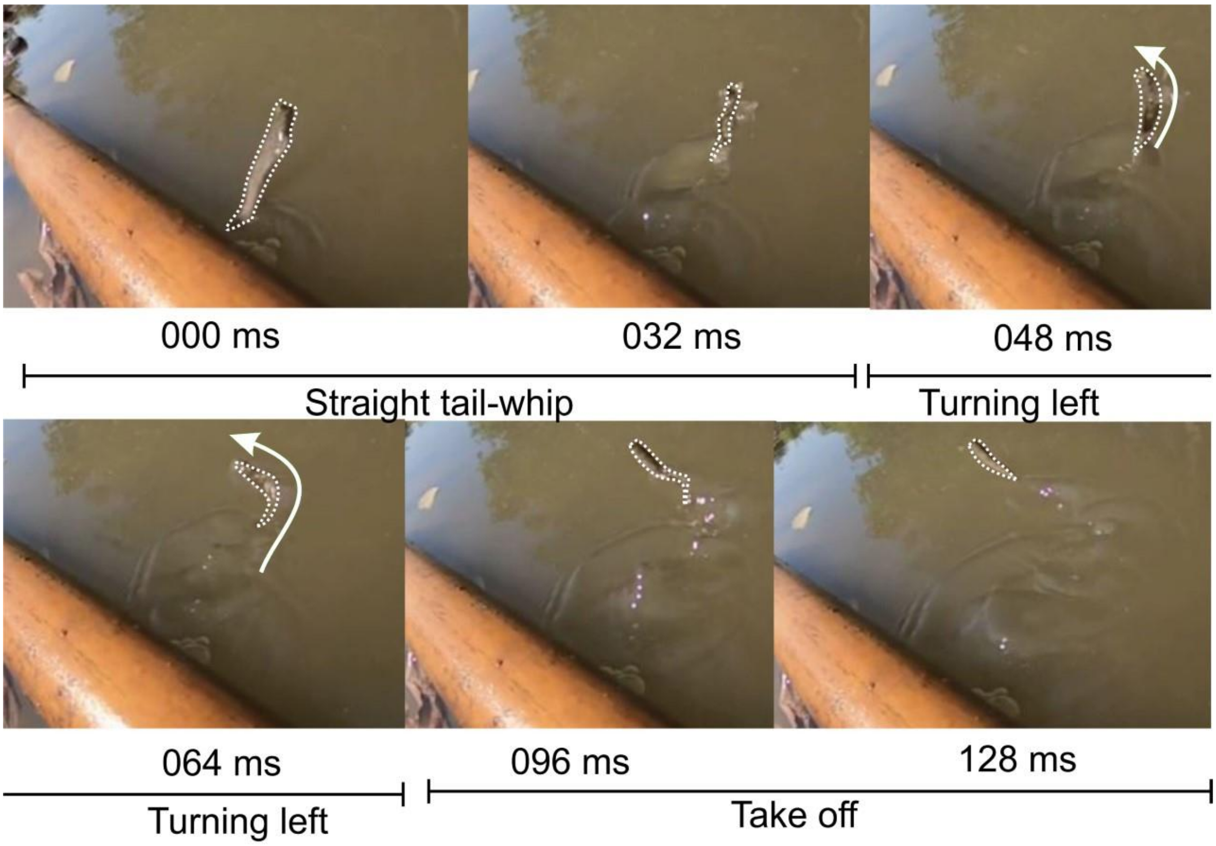

Figure 13. Directional change (white arrow) of *P. variabilis* during a water-hopping sequence (Supplementary Video S6). Sharp changes in direction initiate with the turning of the head, which is followed by a tight caudal bend, after which the mudskipper straightens its caudal by shifting its caudal to the tip, in line with its head. The mudskipper is outlined with white dots.

Figure 14. *P. variabilis* making a short U-turn (white arrow to return to the littoral zone from where it started (Supplementary Video S7). Sharp changes in direction initiate with the turning of the head, which is followed by a tight caudal bend, after which the mudskipper straightens its caudal by shifting its caudal to the tip, in line with its head. The mudskipper is outlined with white dots.

Figure 15. *P. variabilis* hopping from a vertical position onto the water to initiate a water-hopping sequence. The mudskipper first tilts its head in the direction it will hop while its caudal body remains in contact with the substrate, resulting in a $> 90^{o}$ bend of the body. The mudskipper then presses the lateral surface of its caudal fin against the vertical surface and extends it to complete the hop onto the water (see Supplemental Videos S3 and S6 for hops from vertical/inclined surfaces and Supplemental Video S8 for hops from the water onto a vertical surface).

Table 2. Average kinetic measurements of other behaviours as observed from the video footage. Standard deviations are provided in parentheses. Note: Recording was at 240 fps. Information on the number of times each fish was recorded for each behaviour is provided in the Electronic Supplemental Material SM1.

ID (c.f. Fig. 16)	Observed behaviour	Number of fish filmed	Total number of events observed	Distance travelled (cm)	Duration (ms)	Velocity (m/s)
A	Dive to submerged solid substrate	1	1	11.5 (NA)*	174 (NA)*	0.7 (NA)*
B	Hopping on land	3	5	10.3 (± 4.8)	211.8 (± 62.7)	0.5 (± 0.1)
C	Sliding on water surface	4	5	6.9 (± 2.6)	87 (± 56.2)	1 (± 0.5)
D	Sliding from solid substrate into water	6	6	8.6 (± 4.8)	165.8 (± 137.7)	0.9 (± 0.7)
E	Sliding to solid substrate from water	2	2	5.7 (± 4.1)	228 (± 14.1)	0.3 (± 0.2)
F	Swimming at water surface	6	12	18.2 (± 13.4)	393.4 (± 287.7)	0.5 (± 0.3)
G	Taxiing from water to solid substrate	7	9	16.9 (± 8.2)	237.9 (± 140.4)	0.8 (± 0.3)
H	Hopping from a vertical or inclined solid substrate to water	2	3	26.8 (± 8.8)	258.3 (± 64.5)	1 (± 0.1)
I	Taxiing to a change in direction	9	14	13.5 (± 9.1)	169.5 (± 78.7)	0.9 (± 0.5)
J	Taxiing to a U turn returning to littoral	2	5	25.3 (± 5.1)	340.6 (± 63.1)	0.8 (± 0.1)

***Note: There is no standard deviation available for single observations.**

Diving was the least frequently observed behaviour which was noted to follow swimming behaviour (the initial caudal undulation for swimming can be seen in Fig. 16A; t = 0.000 - 0.052 s, after which the mudskipper would submerge underwater (Fig. 16A; t = 0.082 s; Supplemental Video S5 at time 00:06) by initially tilting its head to pitch down under the water. Terrestrial-hopping (Fig. 16B) matches the description of a prone jump in Gibb et al. (2013) in that the mudskipper performs an axial bend by pulling its caudal region laterally towards its head, with the side of caudal region parallel with the solid substrate (Fig. 16B; t = 0.000 - 0.110 s). After this, the mudskipper presses its caudal peduncle onto the substrate (Fig. 16B; t = 0.122 - 0.137 s) to initiate an airborne ascent (Fig. 16B; t = 0.137 - 0.168 s). Other than hopping, the mudskipper occasionally drifts or slides. Sliding is a result of momentum from a previous hop and occurs on the water surface (Fig. 16C). When surface sliding, the mudskipper's body remains straight (Fig. 16C; t =

0.000 - 0.074 s) after which the pectoral fins were noted to extend (Fig. 16C; t = 0.158 s). The mudskipper was also noted to slide from a solid substrate by using one of its pectoral fins to instigate the body slide towards the water (Fig. 16D). The mudskipper was also noted to slide to a stop, from the water to a solid substrate (e.g. tree branch; Fig. 16E) after taxiing or hopping. While sliding to a solid substrate, the mudskipper body posture remained the same through the duration of the slide until it reaches the solid substrate (Fig. 16E; t = 0.000 - 0.027 s). Swimming (Fig 16F) was a rarely observed behaviour since the mudskipper tended to favour water-hopping. The mudskipper performed carangiform type swimming (Budi et al., 2018), in that the mudskipper relies on lateral cyclical body-caudal fin (BCF) undulation using two-thirds of its body, beginning at the posterior region of its cranium and ending at the tip of its caudal fin (Sfakiotakis et al., 1999). Occasionally we noticed the mudskipper taxiing from water directly to a solid substrate (Fig. 16G). The mudskipper would initially align its body towards the solid substrate while taxiing (Fig. 16G; t = 0.000 - 0.183 s) and would decrease in speed on approach the solid substrate by performing an axial bend (Fig. 16G; t = 0.192 - 0.198 s). We noticed on occasion, the mudskipper hopping from a vertical or inclined surface. It conducted this by initially tilting its head towards the water first (Fig. 16H – 0.035 s) before the rest of the anterior body followed the head while its caudal body remained in contact with the surface (Fig. 16H – 0.050 s). This results in a very tight bend in the body of the mudskipper. The mudskipper then pushes the ventral surface of its caudal body against the solid substrate, which launches the mudskipper from the substrate and is followed immediately by the straightening of its caudal body in line with the anterior portion of the fish (Fig. 16H – 0.072 s). When it contacts the water (Fig. 16H – 0.094 s), it immediately commences water-hopping. Hops to a vertical or inclined solid substrate were more rarely observed and one example can be viewed in Supplementary Video S8. Occasionally, during water surface taxiing, mudskippers were observed either performing sharp lateral turns (Fig. 16I) or sharp U-turns (Fig. 16J). Both types of turns involved a headfirst redirection followed by a sharp turn or a sharp U-turn (Fig. 16I; t = 0.012 - 0.025 s and Fig. 16J; t = 0.028 - 0.044 s, for a sharp turn and sharp U-turn, respectively). After this, the rest of the body would follow as the mudskipper would develop a tight bend in its caudal, which was then straightened out from the bend to the caudal fin tip in the direction of the head (Fig. 16I; t = 0.025 s and Fig. 16J; t = 0.044 s, for a sharp turn and sharp U-turn, respectively). Once straightened the mudskipper would continue water-hopping in its new direction (Fig. 16I; t = 0.034 s and Fig. 16J; t = 0.066 s, for a sharp turn and sharp U-turn, respectively).

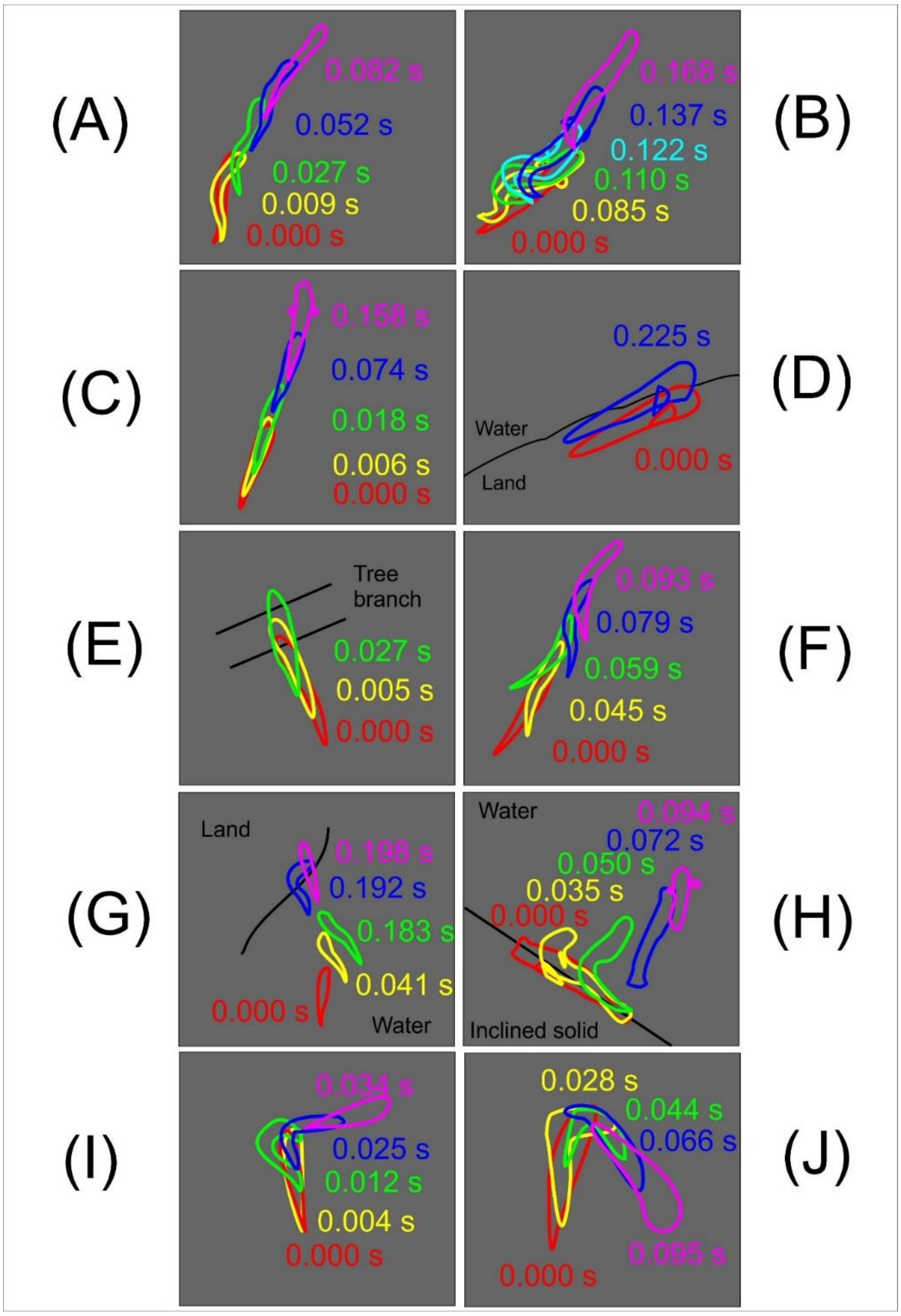

Figure 16. Representative examples of the kinematics of the less frequently observed behaviours of *P. variabilis* as referred to in Table 2 (plan views only). (A) dive to submerged solid substrate (B) hopping on land (C) sliding on water surface (D) sliding from solid substrate into water (E) sliding to solid substrate from water (F) swimming at water surface (G) taxiing from water to solid substrate (H) hopping from a vertical or inclined solid substrate onto water surface (I) taxiing to a change in direction and (J) taxiing to a U turn returning to littoral. Each kinematic step is colour-tagged differently and the times they were recorded are rendered in the same colour.

4. DISCUSSION

During the periods of water-hopping in contact with the water surface, we find that *P. variabilis* will most commonly initiate acceleration by taxiing. This builds up the speed needed to allow them to continue water-hopping. Nevertheless, we also note instances where *P. variabilis* merely bounces off the surface of the water to return to an airborne ascent. The propulsive burst from taxiing results in an increase in velocity when the fish is airborne, which presumably is due to the transition from a hydrodynamic to aerodynamic environment where drag is lower. Taxiing is the primary source of speed for an airborne ascent. It seems plausible to suggest that retraction of the pectoral fins when airborne serves to reduce aerodynamic drag. Interestingly, the lowest velocities are noted for the water bounces on the water surface, indicating that hydrodynamic drag plays a critical role (more so than aerodynamic drag) in slowing the fish down. From a perspective of preserving kinetic energy for a non-taxiing fish (i.e. only bounces), there is therefore an obvious benefit in spending less time on the water surface. This may also be a means of preserving energy.

On a few occasions, the mudskipper makes a sharp turn by taxiing for a short period on the surface of the water, by which means it is able to redirect its path (Fig. 10B and 13; as seen in two out of four fishes, Table 2). A similar ability to change direction during terrestrial jump sequences has also been observed in the intertidal killifish (mummichogs), *Fundulus heteroclitus*, as part of its visual navigation response on land (Bressman et al., 2016). It is possible that directional changes during water-hopping may also be part of a visual navigational response for a mudskipper, indicating the mudskippers possess biologically advanced escape tactics. We observed that mudskippers also keep their heads above water during water turns and when they swim (Fig. 11; Supplemental Videos S4 and S5), as opposed to submerging fully, and we assume that this relates to a reliance on vision. The taxi to take off behaviour observed in *P. variabilis* is somewhat similar to the taxi to take off behaviour of flying fish (Exocoetidae). The flying fish takes a longer time than *P. variabilis* to build-up speed using its tail on the water surface (Franzisket, 1965 *cit.* Davenport, 1994). Its large pectoral fins are used for sliding and the process is supported by the long size of the lower lobe (hypocaudal lobe) of its caudal fin, which helps the fish take off from the water to slide (Dasilao et al., 1997). However, the airborne duration of flying fish depends on a wind-stream (Hubbs, 1937 *cit.* Davenport, 1994) created by the pectoral and pelvic fins. These fins have an angle of incidence of 12° and 5°, respectively, and are used to control the lift while the tail movements generate a forward thrust, which subsequently enables an airborne ascent (Park and Choi, 2010). The kinematics of this behaviour might be similar to the pre-hop taxiing behaviour observed in *P. variabilis,* though flying fish taxi are airborne for longer durations than mudskippers. In this study, *P. variabilis* took on average, 158.8 ms for land-to-water-hopping, 126.9 ms for water-to-water-hopping (normal, with taxiing), and 149.5 ms for water to land, over distances of 11.3 cm, 20.6 cm, and 13.7 cm, respectively (*cf.* Table 1). In comparison, flying fish (*Cypselurus sp.*) remain airborne for 20-30 m over a period of 7-9 seconds (Kawachi et al., 1993). The flying fish flies *ca*. 100 times farther than *P. variabilis*, and for a 70 times longer duration.

The tail movements of *P. variabilis* are similar to those of the flying fish prior to a take-off from the water surface, Figure 17. Both the tail and the caudal fins appear to be of importance for both of these fishes during the take-off that allows them to ascend into the air. The internal musculature of the caudal fin provides a spring-like propulsion during take-off by moving laterally (Fig. 4), which allows the fish to move forward whilst gaining lift for an airborne ascent. The difference is that unlike the flying fish, the mudskipper conducts taxis for only a short period prior to entering an airborne ascent, Figure 15. When the mudskipper lands, the ventral to pelvic region touches down first, either to land on water or onto a solid surface such as a littoral, a tree face, a rock face or a root. The extension of pectoral fins during part of the airborne process is similar to the flying fish. The main difference is that the flying fish uses its wide pectoral fins to sustain its glide when airborne, while *P. variabilis* uses its narrow pectoral fins as it descends from an airborne stage, just prior to contacting the water surface, or a solid substrate. We hypothesise that this may either (a) cushion the mudskipper's landing or (b) enable the mudskipper with a better control of its airborne descent. When taking off from a solid substrate, *P. variabilis* typically uses a J-start (J-shaped launch). The J-shape is potentially a modified C-start (Perlman and Ashley-Ross, 2016) and we presume it is less pronounced in shape than a C-start as the fish needs to propel itself into the air at an angle closer to 30º– see also Supplementary Video S1.

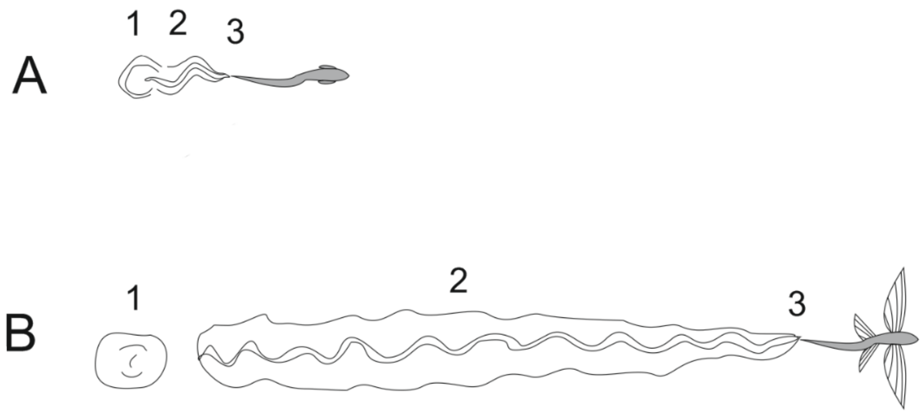

Figure 17. Dorsal view comparison of ripple patterns leading up to take off for *P. variabilis* (A) and a flying fish (B). Initially, concentric ripples are created by the mudskipper as it hops from land to the water (after which it taxis on the surface), whereas for the flying fish these ripples form as the fish emerges from the water (1). The tail for both fish then forms continuous sinuous ripples that essentially propel the fish forward. The mudskipper exhibits a significantly shorter burst during taxiing than the flying fish (2). Finally, the fish takes-off at the end of its taxi (3). The flying fish model shown here is inspired by the work of Franzisket, 1965 *cit.* Davenport, 1994. Supplementary Video S8 shows a longer mudskipper run where ripples patterns are visible.

According to experiments by Rosellini et al. (2005), a flat stone under certain speeds and angles will either skip across the water (bouncing on the water surface), will surf (sliding on the water surface), or will dive (submerge on impact with the water). Using aluminium discs (radius 2.5 cm and height 2.75 cm) and a translation velocity (speed on impact with water) of 3.5 m/s, the disc skips at a 20° angle of impact (ascending angle from the water surface) and a 20° trajectory angle (descending angle from the water surface). The disc surfs at a 30° angle of impact and a 35° trajectory angle. The disc dives at a 35° angle of impact and a 20° trajectory angle. Swanson and Gibb (2004) noted that mudskippers hop (on solid surfaces) at a 35° angle of take-off. Through the image analysis of our video stills, we estimate that *P. variabilis* (analogously) also 'surfs' the water upon impact, reducing its angle while surfing from 28º to 13º. This drop of 15º may increase the contact surface of the fish with water. Unlike a skipping stone, which cannot increase or maintain its speed after contact with the water surface, *P. variabilis* is able to control subsequent hops to some extent through taxiing behaviour. Nevertheless, analogously to the surfing stone, *P. variabilis* does also occasionally bounce on the water surface. During these water bouncing events, the fish reduces its contact time on the water (as compared to a taxi), which in turn decreases the effects of hydrodynamic drag. There are several possible reasons for why during a water bounce, there are variations from hop-to-hop in $K_e(d)$ and K_{e_LOSS}. These might include; *P. variabilis*' entry and exit angles from the water surface for each water-bounce, the depth of water penetration on impact during each bounce, shape factors and their effects on hydrodynamic drag (Bocquet 2003), and of course non-physical factors such as the type and intensity of the escape response exhibited by *P. variabilis*, Domenici et al. (2011a, 2011b).

The pectoral fins are located farther away from the body midline than the pelvic fins, which are closer to the body midline (c.f. Fig. 5A). This location may benefit the mudskipper when landing onto a solid substrate such as a tree trunk, mangrove roots or a rock face, as we presume the mudskipper can more effectively hold onto the substrate when using its pectoral fins, c.f. Figure 5 (B1) in conjunction with its pelvic fins. This benefit is derived from the obvious increase in contact area and a lateral muscular input into the hold, alongside the already beneficial pelvic fin attachment (Wicaksono et al., 2016). When landing onto a littoral, c.f. Figure 5 (B2), we hypothesise that pectoral fin extension may either stabilise the mudskipper on landing, or better prepare it for a subsequent terrestrial movement. It is possible that fin-extension during the airborne period of a water-hop (c.f. Fig. 5 (C-E); Fig. 6 (A-B); Supplementary Video S1), may additionally have an aerodynamic benefit, though we are unsure what the actual purpose for fin extension for a water-to-water hop is, especially since fin-extension was observed in only a few instances.

Mudskippers use water-hopping at least as a means of escape as was evident in this study. The mudskippers studied herein, escaped from us by water-hopping *on almost every occasion*. Logically, it would seem easier for fish to escape a terrestrial threat by submergence and swimming. Rather, *P. variabilis* prefers to hop across the water to another area of land (Supplemental Videos S6, S7 and S8). This may derive from an inherent territorial behaviour (Stebbins and Kalk, 1961; Clayton and Vaughan, 1986) or from the extremely shallow intertidal environments that may not be sufficiently deep to enable escape from terrestrial predators by swimming to depth. Mudskippers live in subterranean mud burrows (Ishimatsu et al., 2007; Larson and Lim, 1997; Graham, 1997), Fig. 18, and as such, instead of escaping by swimming away, we inferred that mudskippers will enter their burrows to escape, particularly if the burrow is nearby. We saw this happen in a few instances, and indeed noted that the mudskippers would tend towards a particular direction, possibly their burrows, even if it meant hopping towards a tree branch with which we approached the fish (threat). Mudskippers retreat to their burrows for protection, but water-hopping is not always followed by a burrow hiding behaviour. Water-hopping allows the mudskipper to get in closer proximity to its burrow, where it can hide if it feels an imminent threat.

Figure 18. *P. variabilis* next to a burrow opening/entrance (indicated by the white arrow).

5. CONCLUSION

Mudskippers (family Gobiidae) are often considered extant examples of how fish have transitioned from water to land. Here, we also reveal a degree of convergence between mudskipper and flying fish (family Exocoetidae) kinematics in terms of water to air transitions. Both will taxi as an effective means to generating the thrust required for an airborne ascent from the water. The flying fish nevertheless will taxi for longer and remains airborne for longer periods. The mudskipper contrarily will most commonly taxi into a short hop, which could be considered a miniature version of the flying fish glide, however there are notable differences. Although *P. variabilis*' water-hopping converges conceptually with the flying fish glide, its kinematic movements occur over a considerably shorter duration and additionally unlike the flying fish, *P. variabilis* does not facilitate a glide using its fins. As such, we consider water-hopping to be an alternative, new form of fish locomotion. Water-hopping has most commonly been observed as initiating from a hop from a solid substrate into the water. As the mudskipper lands on the water surface it thrusts its caudal fin laterally to generate forward momentum, taking it into the air once again. This process of water-hopping (airborne to taxiing to airborne) continues until it reaches another solid substrate. Importantly, we provide evidence that *P. variabilis* is able to initiate a water-hopping sequence from a vertical or inclined solid substrate, and is also able to land onto a vertical or inclined surface from a water-hopping sequence. We postulate that this mudskipper's escape behaviour allows it to remain within an accessible range of its burrow, where it can hide if there is an imminent threat.

ONLINE SUPPLEMENTARY VIDEOS

We have uploaded a number of slow motion videos for the use of Zoology's readership. All videos have been slowed down to 10% of the original speed with the exception of S2 and S8 which are at 5% of the original video speed. Each video is accompanied by a descriptive caption as shown below:

S1– This video shows a sequence of *P. variabilis* taxiing taxiing on the water surface (undulating its caudal body) while water-hopping. The fish starts its sequence from a vertical start position on the side of a mangrove root. The fish can be seen deploying its pectoral fins upon landing on the water surface. Ripple formation can be observed to some extent during some of the hops (filmed at 240fps).

S2– This video shows *P. variabilis* bounce on the surface of the water while water-hopping. We only observed this twice while filming. The fish can be seen slightly left of centre near the top of the screen (filmed at 240 fps).

S3– This video shows *P. variabilis* water-hop from a vertical start position (using a C-start) on the side of a pile. The ripples that form from its contact with the rapidly, leaving behind ripples which are more easily observable than in S1 due to the darker water (filmed at 240fps).

S4 – This video shows *P. variabilis* swim at the water surface before diving and re-emerging from the water into a taxi eventually ascending to the air (filmed at 240fps).

S5 – This video shows *P. variabilis* swimming at the water surface after landed from a water-hop, which is then followed by a dive (filmed at 240fps).

S6 – This video shows *P. variabilis* launch into a water-hopping sequence from an initially vertical position on the side of a fallen bamboo pile. The fish proceeds to water-hop in a zig-zag pattern with radical angular turns, leaving relatively clear ripple formation each time it contacts the water and taxis. The fish eventually hops back onto an inclined pile (filmed at 240fps).

S7 – This video shows perform a U-turn from starting and ending on the same littoral zone (filmed at 240fps).

S8 – This video shows *P. variabilis* launch from a pile into a water-hopping sequence, zig-zagging with less radical angular turns than as seen in S6. Ripples form as described in this paper, though they are harder to see than in S3 (due to contrast and film quality). Importantly, the fish water-hops back into a vertical position onto the side of a wooden pile, which again, indicates that this tree-climbing fish is able to both launch from, and land onto, vertical/inclined terrain such as trees, roots, rock faces, piles (filmed at 60fps).

ELECTRONIC SUPPLEMENTAL MATERIAL

SM1 – This online file provides details on the number of fish filmed and the number of times each fish was filmed for different kinematic behaviours.

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