OPERCULAR JETTING DURING FAST-STARTS BY FLATFISHES

ELIZABETH L. BRAINERD[1,2,*], BENJAMIN N. PAGE[2,†] AND FRANK E. FISH[3]

[1]*Department of Biology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003, USA, [2]Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA* and [3]*Department of Biology, West Chester University, West Chester, PA 19383, USA*

Summary

When attacked by predators, flatfishes perform fast-starts that result in a rapid take-off from the ocean bottom on which they lie. High-speed video recordings of the blind side of flatfishes indicate that they expel a coherent jet of water from the blind-side opercular valve during take-off. Buccal pressure recordings in winter flounder (*Pseudopleuronectes americanus*) show that a buccal pressure pulse begins 0–20 ms before the beginning of the fast-start and has a range of mean magnitudes for three individuals of 1.6–10.7 kPa. We hypothesize that one function of the opercular jet in flatfishes may be to reduce the effects of Stefan adhesion. Stefan adhesion occurs as the fish lifts its head up rapidly from the ocean bottom, when water must flow into the space forming beneath the fish. Water viscosity opposes this rapid shear, and a suction pressure develops under the fish, making it more difficult for the fish to escape from the bottom. To estimate the magnitude of Stefan adhesion, we simulated fast-starts using a physical model in which a dead flounder was pulled upwards with an acceleration of 95 m s^{-2}. Results from the physical model indicate that up to 35 % of the total force required to lift the head at 20 ms into the start can be attributed to Stefan adhesion. Despite this large adhesion force, previous work has shown that live flatfish do not show improved fast-start performance when Stefan adhesion has been eliminated by starting the fish from an open wire grid. Thus, live fishes are likely to be using behavioral mechanisms to reduce the adhesion force. Both the timing and location along the body of the opercular jet indicate that it is ideally suited to attenuate the effects of Stefan adhesion. Propping the body up on the median fins may also reduce adhesion by increasing the initial distance between the fish and the ocean floor.

Key words: Pleuronectiformes, *Pseudopleuronectes americanus*, *Trinectes maculatus*, escape behavior, fast-start, C-start, Mauthner cell, jet propulsion, locomotion.

Introduction

Several groups of fishes have been shown to use or are suspected of using water jets from the opercular valves to aid locomotion (Breder, 1924, 1926; Gregory, 1928; Gradwell, 1971; Weihs, 1977; Fish, 1987; Pietsch and Grobecker, 1987). Most studies of jet propulsion in fishes have been concerned with multiple jets that produce continuous, if somewhat staccato, locomotion. Some sources, however, have suggested that fishes performing fast-starts to escape from predators may produce a single, forceful expulsion of water from the opercular valves (Diamond, 1971; Lagler, 1977; Pietsch and Grobecker, 1987). It also has been suggested that skates and rays use their ventral gill openings to produce a 'sudden, jet-like take off from the bottom' (Clark, 1969, p. 234).

Flatfishes of the order Pleuronectiformes are laterally compressed, benthic fishes that spend their adult lives lying on one side of their bodies on the ocean bottom. Although the orbits and some other cranial structures have become asymmetrical, the gill cavities and gill openings remain essentially symmetrical (Liem *et al.* 1985). Thus, flatfishes have a functional operculum and opercular valve on their blind (bottom) side. It is not known whether flatfishes expel a jet water of out of the blind-side opercular valve during take-off from the bottom but, if they do, this water jet could have different hydrodynamic effects from those in other fishes because water is injected between the body of the flatfish and the ocean bottom on which it lies. Thus, a primary goal of the present study was to determine whether flatfishes expel water from their blind-side opercular valve during take-off.

In order to escape from predators, flatfishes perform a startle behavior that resembles the C-starts of other fishes, but differs from them in that the flatfish begins its start in physical contact
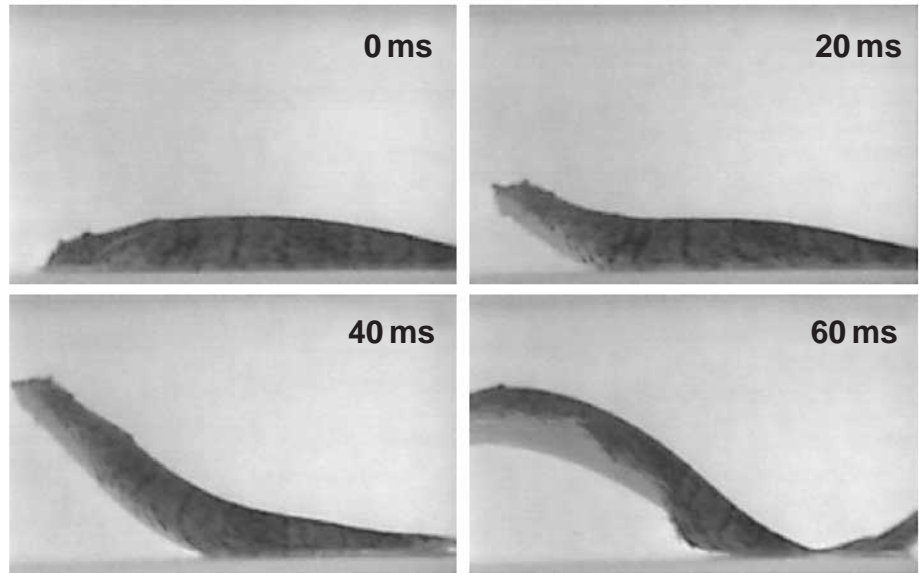
Fig. 1. Escape response of hogchoker (*Trinectes maculatus*). Four fields from a high-speed video recording filmed at 200 fields s^{-1}. The fast-start was elicited by a tap on the caudal peduncle. In stage 1 of the fast-start (0–40 ms), the fish bends its body towards the eyed side and lifts its head and anterior body from the tank bottom. In stage 2 (after 40 ms), the fish curves towards the blind side and begins to move forwards.

with the ocean bottom and uses the maneuver to rise far enough from the bottom to be able to swim away (Fig. 1 and Webb, 1981). Because flatfishes begin their starts in contact with the bottom, it is possible that water viscosity causes significant adhesion, thus making it more difficult for them to escape from the bottom than it is for most other fishes to escape from within the water column. As the flatfish begins to lift its head, water must flow rapidly into the small space that is forming between the fish and the bottom (Fig. 2). This process requires that the water change shape rapidly, a change that is opposed by viscosity. Thus, water will resist flowing under the fish, causing a suction pressure that could make it difficult for the fish to escape from the ocean bottom.

This type of adhesion is called Stefan adhesion after J. Stefan (1874), who first described it. Theoretical expressions for its magnitude are available for some simple geometries, such as circular plates (Wake, 1961, 1982; Denny, 1988). For example, imagine two parallel circular disks very close to each other and submerged in a fluid. The adhesion force (F) as they are separated is directly related to the viscosity (μ) of the fluid,

the radius (r) of the disks to the fourth power and the rate of separation of the disks (dh/dt), and is inversely related to the cube of the instantaneous separation between the disks (h):

$$F = 1.5\pi r^4 (dh/dt)(h^{-3}). \qquad (1)$$

Stefan adhesion force is thus highly sensitive to the size of the objects being separated (r^4) and the separation between them (h^{-3}), and is effective only when the objects are being separated rapidly (dh/dt).

The geometry of a flatfish fast-start suggests that the fish might experience Stefan adhesion as it attempts to take off from the bottom (Figs 1, 2). However, because the fish is irregular in shape, is flexible and peels its body up off the bottom, we were unable to develop a theoretical expression for Stefan adhesion in this situation. It is likely that the force at any instant will have a similar dependence on the dimensions of the part of the fish being lifted, the rate of lifting and the separation as in equation 1, but we were unable to predict the actual adhesion force *versus* time. Thus, we used a physical model of the flatfish fast-start to determine the adhesion force empirically. We then compared the empirically derived Stefan adhesion force with the total vertical force required to perform a fast-start (also measured from the model), and thus determined whether Stefan adhesion can potentially constitute a force large enough to impair fast-start performance in flatfishes.

This study therefore has two goals: first, to determine whether flatfishes jet water from the blind-side opercular valve during fast-starts and, second, to determine whether significant Stefan adhesion force is generated under fast-start conditions. If adhesion is potentially a problem and if flatfishes do, in fact, produce an opercular jet, then it is possible that one function of the jet may be to reduce the adhesion force. Water expelled from the blind-side opercular valve would replace water that would otherwise have to flow into the space between the fish and the ocean bottom, and the opercular jet would thus reduce the suction forming as the fish lifts its head.
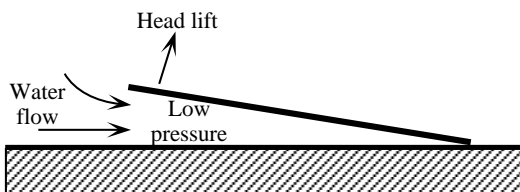

Fig. 2. Conceptual model of Stefan adhesion force caused by proximity to the tank bottom. As the fish lifts its head from the bottom, water must flow rapidly into the small space forming under the fish. The viscosity of the water will resist this high-shear flow, thus producing an area of low pressure under the fish. The low pressure produces an adhesion force that increases the force required to lift the head.

Materials and methods

Experimental animals

We used two species of flatfishes for most of our observations and experiments: American winter flounder *Pseudopleuronectes americanus* (Walbaum), captured off Woods Hole, Massachusetts, and hogchokers *Trinectes maculatus* (Bloch and Schneider), captured in the Gulf of Mexico. The fishes were kept in synthetic sea water in 130 l aquaria, and the bottoms of the holding aquaria were covered with a thick layer of dolomite gravel so that the fishes could bury themselves. Hogchokers were kept at 25 °C and winter flounder at either 15 or 21 °C.

High-speed video recording of the blind side

We used high-speed video recordings to observe the blind-side opercular valve during fast-starts of three hogchokers, *T. maculatus*, 12.0, 12.5 and 11.3 cm in total length (*TL*). In addition, we made observations of three other species for comparison: two winter flounder, *P. americanus*, 27.7 and 26.1 cm *TL*; one southern flounder, *Paralichthys lethostigma* (Jordan and Gilbert), 15.2 cm *TL*; and one peacock flounder, *Bothus lunatus* (Linnaeus), approximately 15 cm *TL*. Each fish was placed in a clear acrylic aquarium, 50 cm×25 cm×30 cm, and the blind side of the fish was filmed from a mirror placed at 45 ° to the bottom of the transparent aquarium. Flatfishes do not show a startle response to auditory stimuli when they are on the bottom (Zottoli, 1981). They do, however, respond to direct mechanical stimuli and we therefore induced the fishes to perform fast-starts either by pushing down suddenly on the caudal peduncle with a finger or by grabbing the caudal peduncle between thumb and forefinger. Video recordings of opercular jetting were recorded at 200 fields s^{-1} using an NAC HSV-200 high-speed video system.

A dye made from food coloring mixed with milk was used to visualize flow out of the blind-side opercular valve during fast-starts. A hypodermic syringe and cannula were used to deliver the dye to an area in front of the mouth, and the normal respiratory movements of the fishes then sucked the dye into their buccal and opercular cavities. When the dye began to appear from the blind-side opercular valve, we removed the cannula and induced a fast-start.

Buccal pressure measurements

We chose to record buccal pressures during fast-starts in winter flounder because hogchokers were too small for the surgical implantation of a buccal cannula. Three winter flounder (*P. americanus*) were used for buccal pressure recordings: flounder 01, 30 cm *TL*; flounder 02, 27 cm *TL*; flounder 03, 29 cm *TL*. The fish were anesthetized with tricaine methanesulfonate (Finquel, Argent Labs, Redmond, WA, USA). A 1.5 mm diameter hole was drilled through the eyed-side entopterygoid, just ventral to the orbit. A 30 cm long polyethylene cannula (Intramedic PE 90, i.d. 0.86 mm, o.d. 1.27 mm) was heat-flared at one end, threaded through the hole and secured with the flared end flush against the lateral wall of the buccal cavity. The fish were then returned to their holding aquarium and allowed to recover for at least 4 h before pressure recordings were made.

Pressure measurements were made with a Millar Mikro-tip pressure transducer (SPR-407, Millar Instruments, Houston, TX, USA), which was threaded down the cannula until the pressure sensor was flush with the opening. The fish were induced to fast-start by pinching the caudal peduncle, and after each start they were allowed to re-bury themselves in the gravel at the bottom of the aquarium and to rest for at least 15 min.

The starts were recorded on high-speed video and synchronized with the pressure recordings to relate the timing of fast-start initiation with the pressure waves. Flounder 01 was kept at 15 °C and videos were recorded at 200 fields s^{-1} using an NAC HSV-200 video system. Flounder 02 and flounder 03 were kept at 21 °C and videos were recorded at 500 fields s^{-1} using a Kodak Ektapro EM1000 video system. Synchronization on the NAC system was accomplished *via* a small light in the video frame combined with a simultaneous square wave recorded along with the pressures. Synchronization on the Kodak system was accomplished by recording the stroboscopic output from the system.

Physical model of flatfish fast-start

In order to build a physical model of winter flounder fast-starts, we needed to know the vertical acceleration achieved by an individual winter flounder during actual fast-starts. Our goal was to estimate the vertical acceleration of the fish during the first 20 ms of the start. We used an NAC HSV-1000 high-speed video system to record five starts from one fish at 500 fields s^{-1}. The same individual for which we measured the acceleration was then killed and used for the dead fish model (*P. americanus*, 27.7 cm *TL*).

From the video recordings, we measured the vertical position of the tip of the snout *versus* time. The resultant displacement curves were parabolic until approximately 20–30 ms into the start, when the curve flattened out and the fish began to decelerate in preparation for stage 2 of the start. This result indicates that acceleration in the vertical direction is roughly constant during the early part of the start. We fitted a second-order polynomial to the first 20 ms of the combined mean position values for the five starts and then double-differentiated the resultant curve in order to obtain a mean acceleration. In addition, we calculated acceleration separately for each of the five starts recorded. We agree with other studies which have concluded that a five-point moving regression is the best way to characterize the rapidly changing accelerations during fast-starts (Harper and Blake, 1989*a,b*; Webb, 1977). In this case, however, we were looking only at the first 20 ms of the start during which the acceleration was fairly constant, and thus a single polynomial regression was sufficient.

We used the calculated accelerations from live fish to build an apparatus designed to simulate fast-starts by pulling a dead flounder off the bottom at a constant acceleration of 95 m s^{-2} (Fig. 3). This acceleration is slightly higher than the mean acceleration measured for our 27.7 cm *TL* fish (82.8 m s^{-2}), but
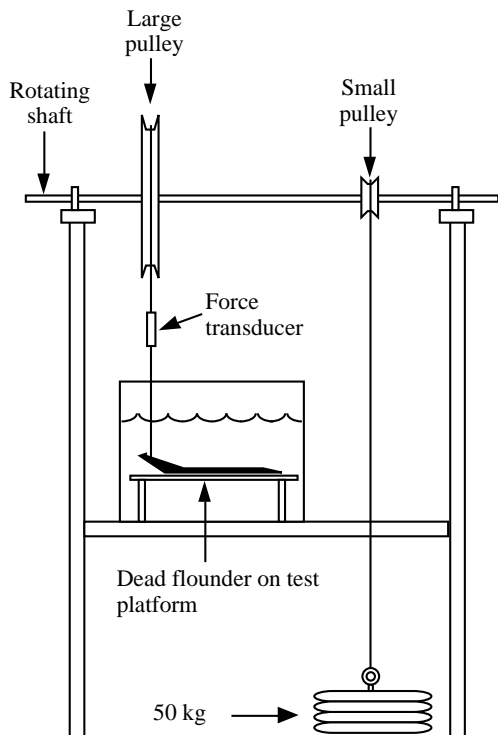
Fig. 3. Apparatus used to measure the force of Stefan adhesion in a dead flatfish. A steel fishing leader cable was connected to the head of a freshly killed winter flounder (*Pseudopleuronectes americanus*). The flounder was placed on a platform in a water-filled aquarium. The cable was connected to a force transducer and then to a large pulley on a rotating shaft. Also attached to the rotating shaft was a small pulley (9.7 times smaller than the large pulley), from which was hanging 50 kg of barbell weights. When the weights were allowed to drop, the head of the fish was pulled upwards with an acceleration of 9.7 times the acceleration of gravity ($95\,\mathrm{m\,s^{-2}}$). The force required to pull the fish off the test platform was measured for an open wire grid (no adhesion force) and compared with the force required to pull the fish up from a sand bottom, a mud bottom and an acrylic bottom. The adhesion force was then calculated as the force required to pull the fish off the sand, mud or acrylic bottom minus the force required to pull the fish off the open wire grid.

slightly lower than the maximum recorded acceleration for this fish ($113\,\mathrm{m\,s^{-2}}$). An acceleration of $95\,\mathrm{m\,s^{-2}}$ was chosen on the basis of the availability of parts for the apparatus (see relative pulley sizes below).

The pulling apparatus consisted of a 1.8 m tall steel pipe scaffold supporting two V-belt pulleys, one large (0.282 m diameter) and one small (0.029 m diameter), on a rotating shaft above an aquarium (Fig. 3). A 490 N weight was attached to the small pulley, and a dead flounder was attached by a long cable to the large pulley. As the weight dropped, it turned the shaft and the large pulley so that the fish was pulled up at a constant acceleration equal to the ratio of the diameter of the large pulley to the diameter of the small pulley times the acceleration of gravity ($9.7\boldsymbol{g}$).

For the model fish, we used the same individual for which we had measured vertical acceleration (*P. americanus*, 27.7 cm

TL, killed with an overdose of tricaine methanesulfonate and used immediately). The fish was attached to the large pulley by steel fishing leader cable which was connected to a hard rubber disc inside the buccal cavity of the fish. The cable exited through a hole drilled in the ectopterygoid and entopterygoid bones on the eyed side of the fish.

The forces generated as the fish was pulled upwards were measured with a Kistler model 9207 force transducer (Kistler Instrument Corp., Amherst, NY, USA), inserted into the cable between the fish and the large pulley (Fig. 3). The output from this transducer was amplified by a Kistler model 5004 dual-mode amplifier and then fed into an analog-to-digital conversion board (MacADios II, GW Instruments, Somerville, MA, USA) in a Macintosh computer. The force traces showed the effect of ringing (vibration) in the steel fishing leader cable at a higher frequency than the main frequency of the pull. This ringing was filtered out of the signals using digital filters in SuperScope II (GW Instruments, Somerville, MA, USA).

Calculation of adhesion force from model results

The purpose of this model was to measure the force required to pull a flounder up from different bottom types: sand, mud, acrylic and an open wire platform. Because water could flow through the bottom of the wire platform, the force required to pull a flounder off the wire platform included a negligible contribution from Stefan adhesion. Therefore, we used the difference between the force required to pull a fish off the test substrata and the wire platform to estimate the force of Stefan adhesion for each test substratum.

We recorded ten pulls from each of four bottom types: a platform of parallel wires, 2.1 cm apart and 12.8 cm above the bottom of the aquarium, an acrylic platform, fine sand from a beach in Quincy, MA, USA, and fine silty mud from the Charles River in Cambridge, MA, USA. Within each substratum type, the force curves for the ten runs were very similar to each other. The individual force traces were aligned using the time that the force first began to increase in each trace. High-speed video recordings synchronized with the force traces showed that, owing to slack in the fishing leader cable, the fish began to move approximately 7 ms after the force first began to rise. Accordingly, we have shifted the zero for the force traces to 7 ms after the force begins to rise. We combined the data from all ten runs on each substratum and fitted the data with the lowest-order polynomial that appeared to follow the force curves closely (a fourth-order polynomial).

Results

Opercular jetting

High-speed video recordings of the blind side revealed that flatfishes open the blind-side opercular valve nearly simultaneously with the beginning of take-off from the bottom (Fig. 4). We recorded 51 starts from the substratum in three hogchokers (*Trinectes maculatus*). In all of these starts, which ranged from relatively slow movements to fast-starts, the blind-side opercular valve opened at approximately the same time as

Fig. 4. Blind-side view of *Trinectes maculatus* performing a fast-start. Two fields from a high-speed video recording filmed at 200 fields s^{-1} using a mirror placed under the glass bottom of an aquarium and angled at 45° to reflect the blind side of the flatfish. The opercular valve is closed in the last frame before movement begins (0 ms). The valve begins to open as the fish begins to move and is fully open by 40 ms into the start.
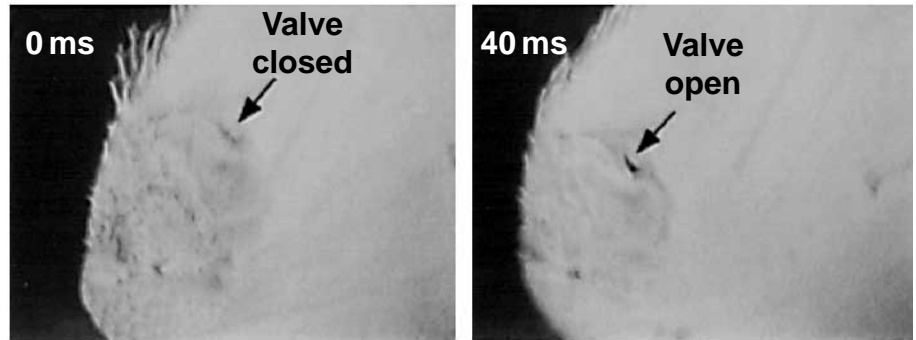
the fish began to move (within 10 ms before or after). For comparison, we recorded blind-side views of starts from three other species. In all of these starts, the opercular valve also opened within 10 ms of the beginning of movement (winter flounder *Pseudopleuronectes americanus*, two individuals, five starts; southern flounder *Paralichthys lethostigma*, one individual, three starts; *Bothus lunatus*, one individual, one start).

To determine whether water is expelled from the open valve during fast-starts, we loaded the buccal and opercular cavities of a hogchoker with dye and then induced fast-starts. Dye was observed to emerge from the opercular valve during the fast-start and often formed a coherent, jet-like stream (Fig. 5). We observed similar dye jets in video recordings of one winter flounder and one southern flounder. We did not notice dye flowing from the eyed-side valve during starts, but we made no video recordings of the eyed side and thus cannot be certain that no water was expelled.

In all four species, we observed that the opercular valve opens during small shifts in position of the fish on the acrylic substratum. In the three species in which we performed dye studies (hogchoker, winter and southern flounder), we also observed dye being expelled from the blind-side opercular valve during these slow maneuvers.

We considered the possibility that the dye observed in Fig. 5 is not expelled by active compression of buccal and opercular cavities, but rather is pulled out by passive suction caused by the reduced pressure under the fish. To determine whether such passive suction plays a role, we recorded buccal pressures synchronized with high-speed video films during fast-starts by three winter flounder. Buccal pressure recordings showed a

large increase in pressure during the fast-start (Fig. 6). In all cases, the head of the fish begins to lift early in the pressure wave, indicating that the jet of dye is caused by active compression of the buccal and opercular cavities. Thus, we conclude that flatfishes actively expel water from the blind-side opercular valve during fast-starts.

It is interesting to note that there are large differences between individual flounders evident in Fig. 6. Although the buccal pressure results for the three individuals are similar in the relative timing of the events, the absolute scales are different. There is an inverse relationship between mean pressure magnitude and mean duration of the pressure wave: in flounder 01, the pressure wave is long and has a low magnitude, whereas in flounder 03 the pressure wave is very short and has a high magnitude. Flounder 01 was kept at a lower temperature (15°C) during recording than flounders 02 and 03 (21°C), which may account for some of the variability.

Adhesion force

We measured the force required to produce simulated fast-starts from different substrata using the apparatus shown in Fig. 3. In order to make the simulated starts realistic, we designed the apparatus to lift a dead fish with a similar vertical acceleration to that achieved by the same fish during natural fast-starts. The mean acceleration achieved by the live fish was 82.8 m s^{-2} (Fig. 7). The apparatus was designed to accelerate the dead fish at 95 m s^{-2}. The actual acceleration of the model was slightly higher than 95 m s^{-2} early in the start and slightly lower later in the start (Fig. 7).

The model apparatus produced starts in which the curvature of

Fig. 5. Dye is ejected through the blind-side opercular valve of *Trinectes maculatus* during a fast-start. Two fields from a high-speed video recording filmed at 200 fields s^{-1} from a mirror placed under the glass bottom of an aquarium and angled at 45° to reflect the blind side of the flatfish. Dye (milk with food coloring) was delivered to the front of the mouth and sucked into the buccal and opercular cavities by normal respiratory movements. During the fast-start, compression of the buccal and opercular cavities ejected a coherent stream of dye from the opercular valve.
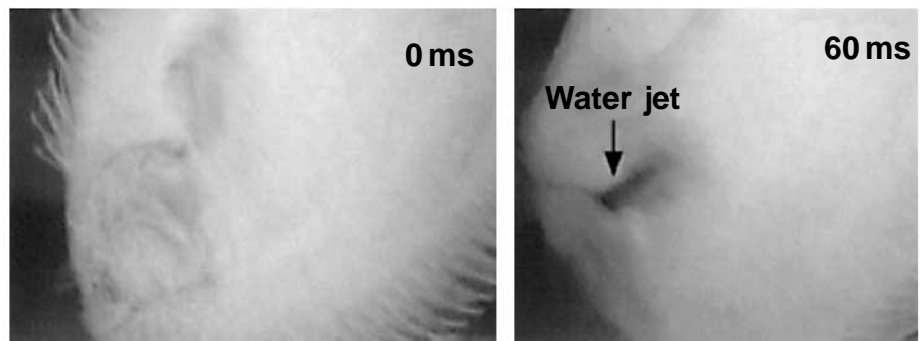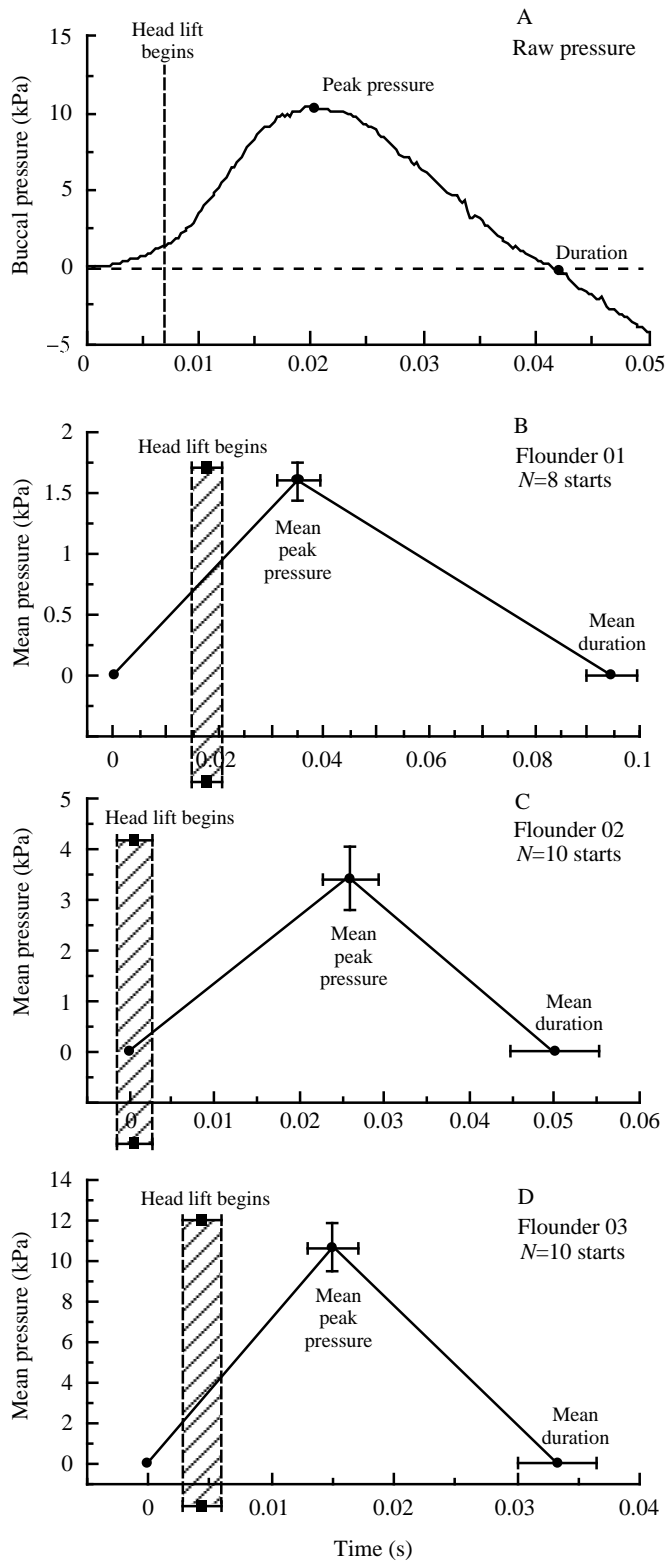
Fig. 6. Buccal cavity pressures during fast-starts in winter flounder (*Pseudopleuronectes americanus*). Buccal pressures were synchronized with high-speed video recordings of the fast-starts. Four variables were measured from each synchronized pressure trace and high-speed video recording: the time from the beginning of the pressure increase to the beginning of head-lifting in the video, the time to peak pressure, the magnitude of the peak pressure, and the duration of the increased pressure. Means and standard errors for these four variables are given for three individual fish in B–D. (A) Raw pressure trace from flounder 03 showing the measured variables. (B) Mean values for flounder 01. (C) Mean values for flounder 02. (D) Mean values for flounder 03. Note that the shapes of the graphs between individuals are similar, but that the scales are different. Between individuals, there is an inverse correlation between pressure duration and magnitude.
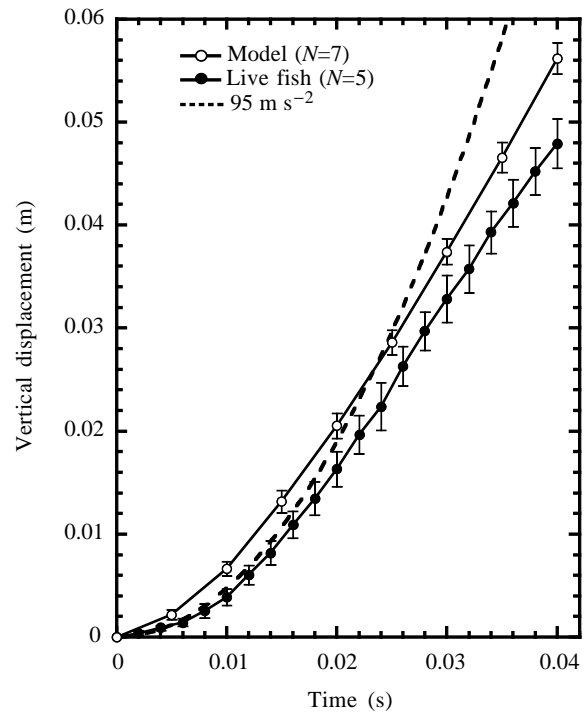

Fig. 7. Vertical displacement curves demonstrating the relative vertical acceleration of a live winter flounder (*Pseudopleuronectes americanus*), our physical model (the same fish, dead) and a curve representing $95\,\mathrm{m\,s^{-2}}$. Symbols represent the mean vertical position of a point near the tip of the snout and error bars are one standard error ($N=5$ starts for the live fish and $N=7$ model starts). The live fish was recorded using a high-speed video at 500 fields s^{-1} and the model was recorded at 200 fields s^{-1}. The model was designed to accelerate the dead fish at $95\,\mathrm{m\,s^{-2}}$. The actual model acceleration follows the theoretical curve for $95\,\mathrm{m\,s^{-2}}$ fairly well, slightly overshooting early in the start and undershooting later on.

the fish looked very similar to that observed in natural fast-starts (Fig. 8). In natural fast-starts, however, the winter flounder began to decelerate in preparation for stage 2 at approximately 20 ms into the start, whereas the model kept accelerating upwards. Thus, the simulated fast-starts are comparable to natural fast-starts only

for the first 20 ms. At 20 ms, the heads of both the model and the live fish have been raised only a short distance, less than 2 cm, above their starting positions (Figs 7, 8).

Force traces from individual runs of the model were highly reproducible on the open wire grid and somewhat more variable on a natural substratum such as sand (Fig. 9A). Variability on
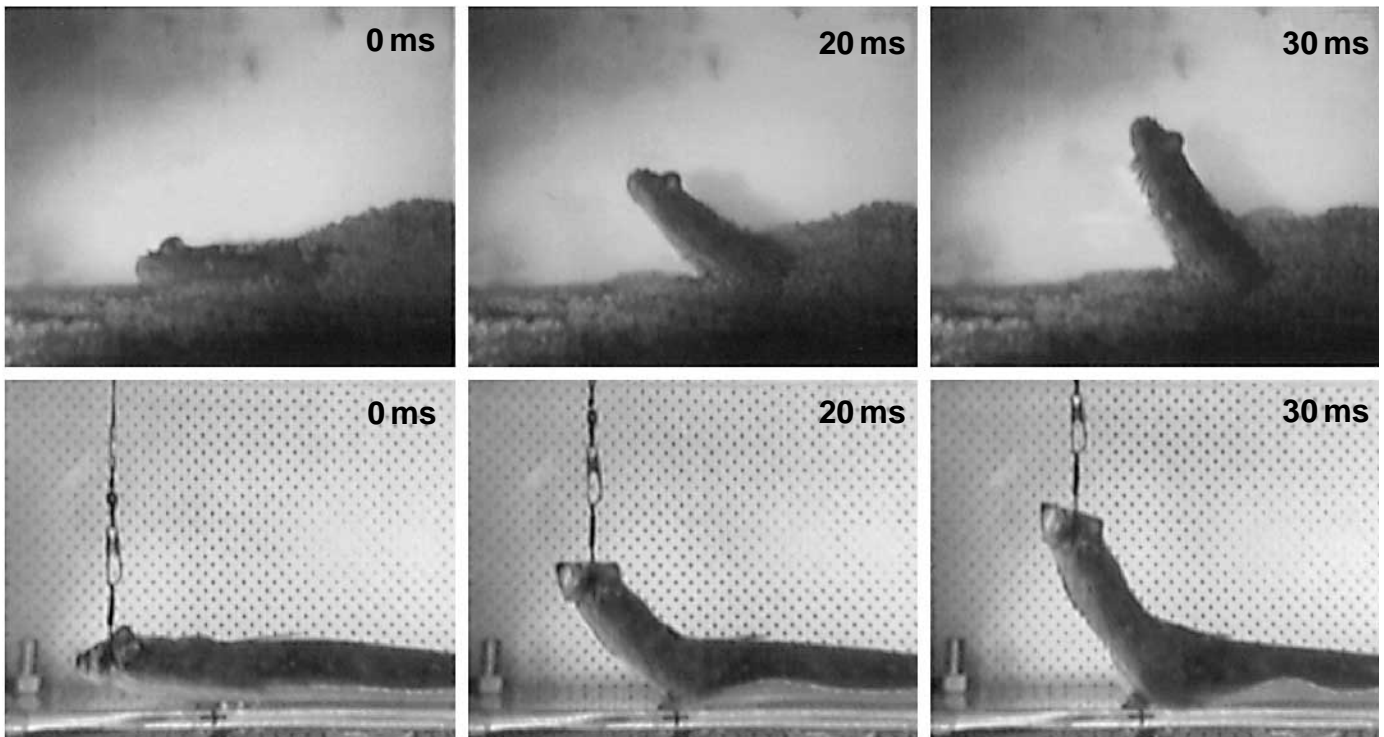
Fig. 8. Fast-start of live winter flounder (top) compared with a simulated fast-start of the physical model (bottom). Note the close similarity in shape and position of the fish between the real fast-start and the simulated fast-start. The main difference is that, in our model, the mouth opens and the jaws protrude in response to the wire cable pulling on and abducting the suspensorium.

the acrylic substratum was similar to that on the grid and variability on the mud substratum was similar to that on sand. The higher variability on sand and mud than on acrylic and the grid may have been due to differences in the configuration of the bottom between trials on these deformable substrata.

It is clear from both the raw traces and the regressions that more force is required to pull a dead flounder off the solid substrata than off the open wire grid (Fig. 9A,B). Subtracting the line for the open wire grid (no adhesion) from the line for each solid substratum yields graphs of adhesion force *versus* time (Fig. 9C). Dividing the adhesion force by the total force required to produce the start gives the percentage of the total force that is attributable to Stefan adhesion. As the fish begins to move, the proportion of force attributable to Stefan adhesion is approximately 15 % on all substrata. The adhesion force rises most rapidly on the sand substratum, reaching 35 % of the total force at 20 ms. Adhesion force rises more slowly on mud, reaching 27 % of the total force at 20 ms. Adhesion force on the acrylic substratum did not rise early in the start but rose sharply later in the start to reach 21 % of the total force at 20 ms.

Discussion

Our results demonstrate that flatfishes open their opercular valve and forcibly jet water out during fast-starts from the bottom (Figs 4–6). Dye that has been placed in the buccal cavity is forcibly expelled in a coherent stream during the start (Fig. 5). Results from buccal pressure measurements synchronized with high-speed video recordings show that the buccal pressure pulse and head lifting begin at approximately the same time (Fig. 6). We also observed that flatfishes expel small puffs of water from the blind-side valve when they shift position on the substratum. This behavior appears to allow them to move easily on a cushion of water, until they clamp the median fins down again as part of their station-holding behavior (Arnold and Weihs, 1978; Webb, 1989).

It is unclear whether the fast-starts that we elicited in our study were Mauthner-cell-initiated. Fishes are able to use several neural pathways to produce kinematically similar escape responses that are collectively called 'fast-starts' (Eaton *et al.* 1982; Jayne and Lauder, 1993). If some or all of our fast-starts were indeed Mauthner-initiated, then it is not surprising that an opercular jet was produced in these starts. It has long been known that fishes compress the buccal and opercular cavities during Mauthner-initiated fast-starts and 'a brief jet of water is discharged backwards from both gill clefts' (Diamond, 1971, p. 278). The Mauthner axon sends motor branches to the cranial and extrinsic eye muscles as well as to the trunk musculature. Contralateral inhibition causes the trunk musculature to be activated unilaterally, thus producing rapid bending of the body to one side. Unlike the trunk musculature, however, the eye and cranial muscles are activated bilaterally (Diamond, 1971; Hackett and Faber, 1983; Eaton and Hackett, 1984).

It is interesting to note, however, that we observed jets of water both during fast-starts and during slow repositioning of the body on the acrylic substratum. Thus, although opercular
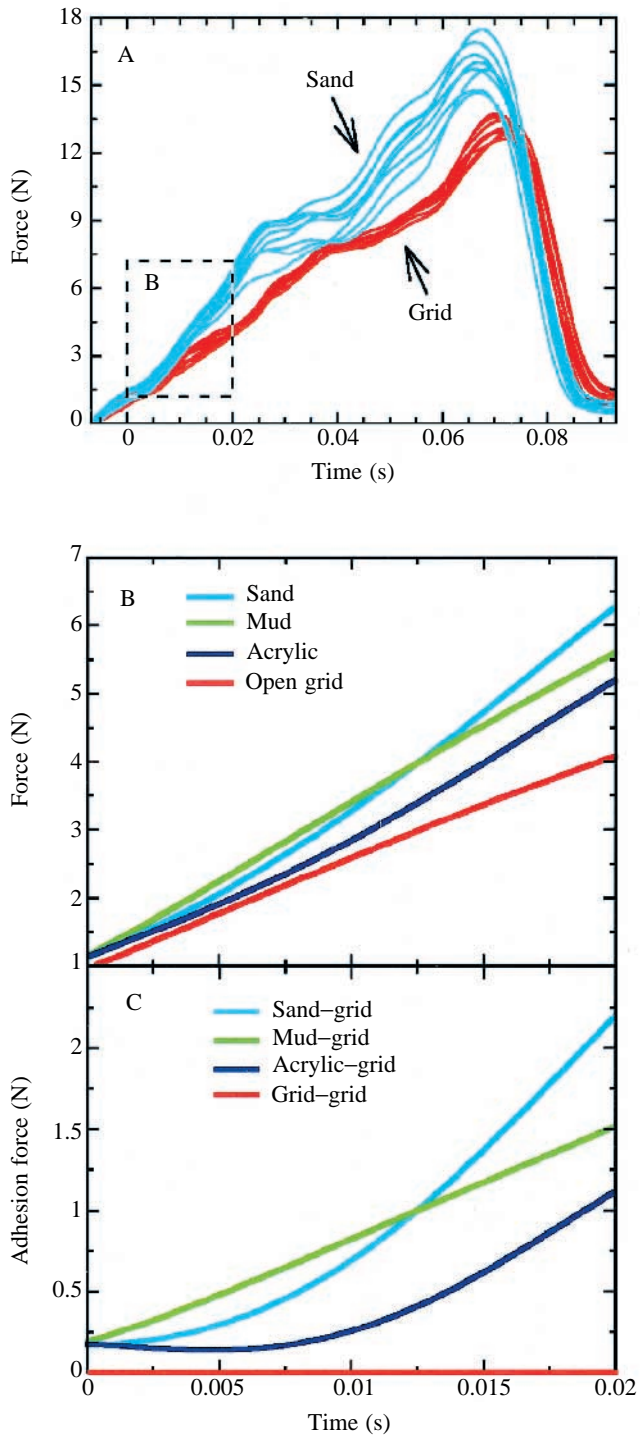
Fig. 9. Force required to pull a dead flounder up from different substrata. (A) Ten raw force traces each for sand and open wire grid substratum. Only the first 20 ms of each pull are equivalent to a natural fast-start because live winter flounder begin to decelerate in preparation for stage 2 at approximately 20 ms after the beginning of movement. The force peaks and falls at approximately 70 ms as the barbell weights hit the ground. The cable to the fish contained some slack, and thus zero time is corrected to 7 ms after the weight began to fall, which was the time when the model actually began to move. (B) Polynomial curve fits to the first 20 ms of ten trials from each of four substrata (sand, mud, acrylic and grid). Fourth-order polynomial curve fits were used because this was the lowest-order polynomial that appeared to follow the contours of the force traces. Note that 15–35 % more force is required to pull the fish up from the sand, mud and acrylic bottoms than from the open wire grid bottom. (C) Adhesion force on sand, mud and acrylic substrata. Adhesion force was calculated by subtracting the open wire grid force from the force on each of the other substrata (assuming negligible Stefan adhesion on the open wire grid).

required to perform a fast-start. From silicone casts of the buccal and opercular cavities of a 0.4 kg winter flounder, we estimate that the fish expels no more than 10 ml (0.01 kg) of water during a fast-start. Thus, the maximum mass of water expelled is at least 40 times smaller than the mass of the fish. By conservation of momentum, one would not expect this relatively small mass of water to have a large effect on the acceleration of the whole fish. The water jet could affect the relatively smaller mass of the head as it is being lifted, but an analysis of this possibility is beyond the scope of this paper.

Adhesion force attenuation by the opercular jet

Results from our physical model indicate that a large proportion of the total force required to produce a simulated fast-start in a dead flounder (up to 35 % at 20 ms into the start) may be attributable to Stefan adhesion (Fig. 9B,C). This result is based on the assumptions that there is negligible adhesion on an open grid and that the additional force required to pull the fish up from the three solid substrata (sand, mud and acrylic) is attributable to adhesion caused by the proximity of a solid substratum. The finding that adhesion forces can be so large in relation to total force suggests that adhesion could be a significant problem for flatfishes escaping from the ocean bottom.

A previous study measured the fast-start performance of a flatfish (*Citharichthys stigmaeus*) in the water column, on a wire grid placed against a solid bottom, and on a grid placed at various distances above the bottom (Webb, 1981). The purpose of Webb's study was to investigate positive effects that the proximity of the fish to the bottom might have on performance (ground effect), and he did not consider the possibility that the bottom might have a negative effect caused by Stefan adhesion. In the comparison of water-column starts with starts from the grid, Webb (1981) found higher acceleration on the grid, which was attributed to the ability of the fish to push off from the grid rather than relying on water reaction forces. In the comparison between starts from the grid on the bottom and starts from the grid positioned above the bottom, no significant difference in

jetting during fast-starts may be stimulated by the Mauthner cell, it appears that flatfishes can voluntarily produce small jets of water for routine movements on the substratum.

What, if any, are the implications of the opercular jet for the mechanics of fast-starts in flatfishes? In this study, we explore the possibility that the water jet may reduce the force of Stefan adhesion during rapid take-offs. The water jet could, however, also assist fast-starts by generating thrust to assist the axial musculature in lifting the head (jet propulsion). We suspect, however, that this force is small relative to the total force

performance was found (performance was measured as the time required to complete stage 1 of the fast-start).

It is revealing to interpret Webb's (1981) results in the light of our finding that Stefan adhesion was large in the simulated fast-starts. In Webb's study, fish starting from the wire grid above the bottom should experience no Stefan adhesion and, thus, would be expected to have a better fast-start performance than those starting from the grid on the bottom. Webb found no difference, however, in performance between the grid and the solid bottom. Thus, Stefan adhesion does not appear to affect fast-start performance in live fishes, and this result indicates that live fishes may be using behavioral techniques to reduce the adhesion force in natural fast-starts.

Two behaviors that would reduce adhesion are the use of the median fins to prop the body up off the bottom and the expulsion of water from the blind-side opercular valve. Flounders do not normally lie flat on the bottom, but rather prop themselves up slightly using the median fins (Stickney *et al.* 1973; Arnold and Weihs, 1978; Webb, 1989). This posture increases the initial separation between the body and the bottom and, since Stefan adhesion is inversely proportional to the cube of the separation (h^{-3}, equation 1), the adhesion force may thereby be reduced. It is likely that propping behavior reduces adhesion of the head region to the bottom, but it may not be effective farther back on the body. Early in the fast-start, the area of the body behind the head is pushed down into the substratum by recoil from the upward head movement (Fig. 1, 20 ms; Webb, 1981). Thus, recoil from head movements causes the separation between the cranial trunk region and the bottom to be very small, and the fish could experience relatively large adhesion forces when this region just behind the head is lifted later in the start.

It seems likely that, in live fishes, the water jet that is forced out of the blind-side opercular valve may reduce the Stefan adhesion in this critical area. The water jet could replace water that would normally have to flow rapidly into the small space forming as the body peels up from the bottom and could thus reduce the adhesion caused by water viscosity.

It is also interesting to note that the center of mass of flatfishes is displaced slightly forwards during stage 1 of fast-starts (Fig. 1 and Webb, 1981). As the fish lifts its head upwards and backwards, reaction forces tend to slide the fish slightly forwards. This forward motion combined with the jet from the opercular valve would tend to help to force a cushion of water under the fish to reduce adhesion. We observed forward sliding during the latter part of stage 1 in live fishes and in our simulated starts. We have not, however, included horizontal accelerations or forces in the analysis of live or simulated fast-starts because our focus has been the early part of stage 1 (0–20 ms), and horizontal displacement is small during this period (Fig. 8).

Detailed consideration of force traces from the model

Only the first 20 ms of the simulated fast-start are comparable to a natural fast-start. After 20 ms, the live fish begins to decelerate in preparation for bending in the opposite direction during stage 2 of the fast-start. In addition, the first 7 ms of the force traces from the simulated starts are also not comparable to natural fast-starts. Despite persistent efforts, we were unable to eliminate all slack in our apparatus and, thus, during the first 7 ms of the simulated start, the slack in the fishing leader cable attached to the fish was being taken up (based on observations of the model with high-speed video recordings). The fish experienced a small force during this time, and thus was probably beginning to move a little, but it was not experiencing the full pull of the weights. In order to correct for the slack, we offset zero time on the force traces to 7 ms after the force began to rise (Fig. 9).

Slack in the cable accounts for the acceleration of the dead fish being higher than $95\,\mathrm{m\,s^{-2}}$ early in the start (Fig. 7). The weights had a non-zero velocity when the cable became taught, and thus the fish was accelerated rapidly to catch up with the weight. In addition, the acceleration of the model was lower than $95\,\mathrm{m\,s^{-2}}$ later in the simulated start (Fig. 7). This difference was probably caused by the force exerted by the fish on the weight. At 20 ms into the simulated start, the fish exerted a pull of 4.0–6.2 N depending on the substratum (Fig. 9). The gear ratio of the pulleys translates this value to a force of 39 N for the grid substratum and 60 N for sand. We calculate that the difference in the force exerted by the fish caused the acceleration of the weight to be 4.4 % lower on sand than on the grid, thus causing us to underestimate slightly the Stefan adhesion force.

It is interesting to speculate about the individual components of the force traces in Fig. 9. The components of the total force are several and change rapidly over time during the start. Total force on all four experimental substrata consists of the force required to accelerate the mass of the fish, the force required to accelerate a mass of water around the fish and drag forces. In addition, the three solid substrata, sand, mud and acrylic, will have a component of force from Stefan adhesion.

Early in the start (0–5 ms), most of the force probably comes from accelerating the mass of the head and surrounding water. During most of this time, the velocities are fairly small, and the total displacement (d) is only 1 mm (from video recordings and equations of motion: $d=1/2at^2$, where a is acceleration and t is time). Thus, drag forces and Stefan adhesion forces are small because velocities are small. In Fig. 9C, Stefan adhesion force is not zero at time zero because the fish already had a small vertical velocity (see above discussion of cable slack). As velocity increases during the start, drag and Stefan adhesion forces are expected to increase. We found that Stefan adhesion forces increase throughout the simulated start, even past the 0–20 ms time range that is comparable to a natural start (Fig. 9A, the difference in force between the sand and grid substrata is attributable to Stefan adhesion). This result is not unexpected, because part of the body remains in contact with the bottom as the fish is peeled up. The increase can be attributed to two factors: the area of the fish in contact with the substratum increases as the peeling region moves caudad and the depth of the fish increases (r in equation 1 increases), and the velocity at which the region of contact is being pulled up increases ($\mathrm{d}h/\mathrm{d}t$ increases, see equation 1).

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Acceleration reaction forces of the fish and water are also expected to increase during the simulated start. Even though acceleration was approximately constant, the mass of the fish being accelerated increased as the fish was pulled higher (as more of the body was pulled up), and thus the inertial force required to accelerate both the fish and the surrounding water increased throughout the start.

The finding that the adhesion force was smaller on acrylic than on sand or mud was unexpected (Fig. 9B,C). We believe, however, that this result may be due to a methodological problem. On sand and mud, we pushed the fish down onto the bottom before each simulated start, thus conforming the substratum to the shape of the fish. This technique was obviously not possible on acrylic, and thus much of the fish's body did not rest as close to the bottom on acrylic trials as it did in the sand and mud trials. Since Stefan adhesion depends on the inverse cube of the height above the bottom (h^{-3}, equation 1), this difference in separation could have had a large effect on the early part of the start. It makes sense that adhesion would increase later in the start as the middle portion of the fish is pushed down onto the acrylic by recoil from the head movement.

The following conclusions may be drawn. (1) Flatfishes expel a jet of water from the blind-side opercular valve during both fast-starts and slower shifts of position on the substratum. (2) A physical model of fast-starts indicates that up to 35 % of the total force required to lift the head early in the start can be attributed to Stefan adhesion. (3) Live flatfishes do not show impaired fast-start performance when started from a solid substratum *versus* an open wire grid (Webb, 1981). Thus, live fishes are likely to be using behavioral mechanisms to reduce the adhesion force. (4) Both the timing and the location along the body of the opercular jet indicate that it is ideally suited to attenuate the effects of Stefan adhesion. Propping the body up on median fins may also reduce adhesion, particularly for the head region early in the fast-start.

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