

THE EFFECT OF THE BOTTOM ON THE FAST START OF
FLATFISH *CITHARICHTHYS STIGMAEUS*

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ABSTRACT

Fast starts of the speckled sanddab, *Citharichthys stigmæus*, were initiated by a 1 volt per centimeter direct current electric shock and recorded on movie film at 250 frames per second. Observations on kinematics and performance were made for fast starts of fish accelerating in the water column and from a grid located at a distance of 0, 1, 3, or 6 cm above the true bottom. During acceleration the body was bent into a U-shape relative to the bottom. The body sustained a direct push against the grid when accelerating from that grid. The amplitude of propulsive movements of fish accelerating from the grid was larger than acceleration movements of fish in the water column away from the bottom, because the potential for energy wastage due to recoil of the body was prevented by the grid. The distance between the grid and the bottom had no effect on fast starts, ruling out any hydrodynamic ground effect. Motion of fish accelerating in the water column was continuous and predominantly in the horizontal plane. There was little motion of fish accelerating from the grid until they started pushing against that grid. Motion was predominantly in the vertical plane. The resultant distance traveled by fish accelerating from the grid, measured at the end of the principal acceleration period exceeded that of fish accelerating in the water column. Velocities and acceleration rates were highest for fish accelerating from the grid. It was concluded that contact with the sea bottom would enhance fast-start performance of flatfish.

Fish of the order Pleuronectiformes are unique because the adults lie on one side. The habit of inclining to one side is common among other benthic fish that are normally vertically oriented, but no other group shows the specialized morphological adaptations of flatfish. Various observations on benthic fish suggest that inclining the body or lying on one side is advantageous for camouflage and crypsis (Norman 1966). Large locomotor advantages could also accrue, especially to flatfish orienting their body axis parallel to the ground.

Improvements in locomotor performance of flatfish could occur through two mechanisms: hydrodynamic ground effect and pushing against a rigid substrate. The hydrodynamic ground effect occurs through interaction of the downwash from propulsive surfaces with the ground (i.e., the sea bottom) and increases effective thrust and decreases effective drag (Bramwell 1976; Lighthill 1979). It has been described for birds (Withers and Timko 1977) and for pectoral fin propulsion of the mandarin fish, *Synchropus picturatus* (Blake

1979). Pushing against the substrate is obviously more energy efficient than pushing against water because more muscle power is converted into body motion rather than wasted in accelerating fluid. It is utilized by macrurous decapods (Webb 1979). The relative importance and effectiveness of these mechanisms will depend on how flatfish move their bodies near the ground.

The following experiments were performed to determine if the sea bottom could influence fast-start (acceleration) movements and performance of a typical flatfish. Emphasis was placed on fast starts because of their importance in evasion of predators and in catching elusive prey (Eaton and Bombardieri 1978; Webb and Skadsen 1980).

METHODS

Fish

Speckled sanddab, *Citharichthys stigmæus* Jordan and Gilbert (family Bothidae) were used. Fish were caught in dip nets by divers along the southern California coast, hence avoiding the damage typical of trawl-caught specimens. Fish were held in a 60,000 l tank at 14° C. They were fed twice a week on frozen brine shrimp.

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Procedures

Individual speckled sanddabs were starved for 24 h. Each fish was lightly anesthetized (MS-222)² and a white thread was sewn above the center of mass of the stretched-straight body calculated from previous measurements on a subsample of fish. This reference facilitated later film analysis. Each fish was then placed in an observation arena and allowed to recover for 24 h overnight.

The observation arena consisted of a chamber 45 cm long, 30 cm wide, and 40 cm deep. A fast start is a short duration stereotyped activity during which fish travel short distances but accelerate at high rates to reach large speeds (Eaton et al. 1977; Webb 1978). The size of the arena would not interfere with fast-start activity but would prevent sustained high-speed swimming. This study is concerned only with the former activity.

The observation chamber had a false bottom made from a wire grid (2.5 cm squares made from 0.08 cm diameter wire). A solid bottom was located beneath the grid and could be set 0, 1, 3, or 6 cm beneath. Comparison of performance during fast starts with the grid set at various distances above the solid bottom was expected to show the importance of the hydrodynamic ground effect as differences in performances once physical contact with the grid had ended. Vertical reinforcers prevented the grid from acting as a spring when a force was applied by an accelerating fish. The observation chamber also allowed room for fish to swim in the water column for short distances permitting observation of fast starts in the water column remote from all possible ground interaction.

The bottom was located in one of the four positions beneath the grid while the sanddab became accustomed to the chamber overnight. Next morning a 1.0 V/cm d.c. electric shock was used to initiate a fast start either from the grid or when the sanddab was temporarily stationary in the water column clear of the grid and bottom. All experiments were performed at 14° C.

Fast starts were recorded on movie film at 250 frames/s. A 45° mirror above the observation chamber allowed simultaneous observation of top and bottom views. A floating lid prevented surface ripples distorting the top-view image.

Each fish was killed after an experiment. The body outline was traced on paper. Mass, total

length, wetted surface area, location of the center of mass, and muscle mass were measured as described by Webb (1977).

There were no differences in these morphometric characteristics among various groups of speckled sanddabs. Combined values were (mean \pm 2 SE); mass, 28.96 \pm 3.78 g; length, 13.7 \pm 0.6 cm; the center of mass, located 5.2 \pm 0.2 cm from the nose; wetted surface area, 120 \pm 10 cm²; muscle mass, free of skin and scales, 11.78 \pm 2.28 g.

Movie film was analyzed frame by frame to observe kinematics and to measure performance. Details are given by Webb (1978). Briefly, performance was measured for the motion of the center of mass of the stretched-straight body. This point approximates the instantaneous center of mass of the flexing body which is the point about which propulsive forces act. Coordinates for motion of the center of mass were measured in the horizontal and vertical planes. The resultant motion of the center of mass was calculated. Velocities and acceleration rates for these three motions (horizontal, vertical, and resultant) were calculated using moving point linear regression methods. Performance parameters were compared using the *t*-test, and significant differences between means are declared at the 5% level.

RESULTS

Kinematics

There were no differences in kinematics of fish accelerating from the grid set at various distances above the solid bottom. Fast-start kinematics for acceleration from the grids (Figure 1) showed the normal three stages originally described by Weihs (1973). During stage 1, the body was bent into a U-posture (0-80 ms in Figure 1A) comparable to the C-posture of other teleosts when viewed from above (Eaton et al. 1977; Webb 1978). The center of mass showed some recoil (i.e., lateral movement in the opposite direction to the tail, and normal to the fish axis) towards the grid because the fish adopted a posture with the body raised by the median fins before a fast start (Stickney et al. 1973). The body was always bent away from the bottom.

During stage 2 (80-120 ms in Figure 1A), the body was bent in the direction opposite to that of stage 1 as the body curvature traveled caudally along the body. Some point of the body remained in contact with the grid almost to the end of stage 2.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

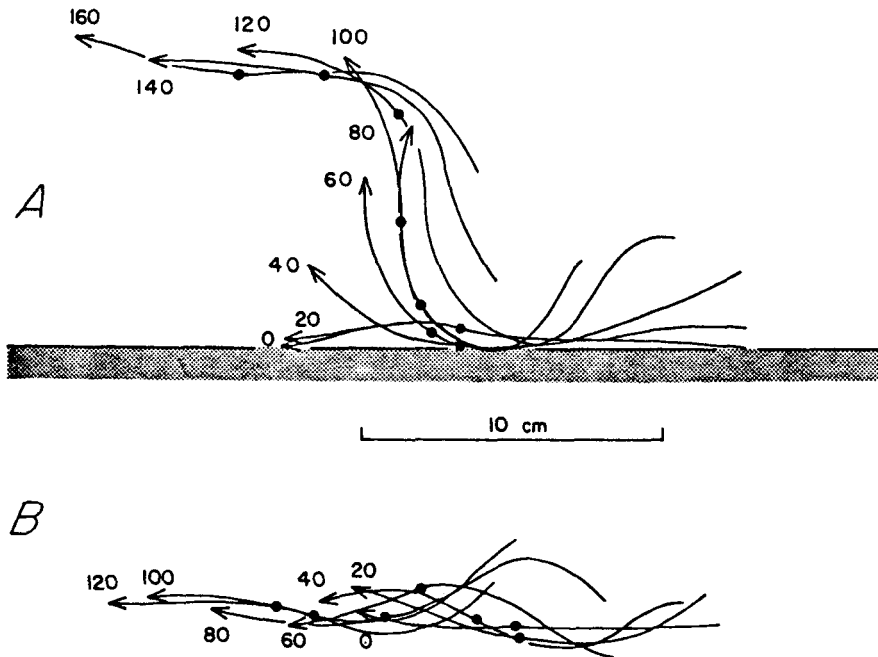


FIGURE 1.—Tracings of the body center-line (seen from the side) at 20 ms intervals to show the acceleration movements during fast starts of *Citharichthys stigmaeus*: A) Acceleration from contact with the grid. B) Acceleration in the water column. Dots show the location of the center of mass of the stretched-straight body. The extended and variable stage 3 following the major acceleration strokes has been omitted for clarity.

The center of mass was propelled vertically away from the ground.

Fast start stage 3, occurring after the major acceleration period, was variable, ranging from an unpowered glide to continued swimming with caudal propagation of propulsive waves sustained from the starting curvature in stage 2.

A typical fast start of a sanddab in the water column away from the bottom is illustrated in Figure 1B. Fast starts in the water column showed the same stages as fast starts from the grid. The amplitude of body movements was usually smaller than those of fish accelerating from the grid. Center of mass recoil, reduced during acceleration from the grid, was observed for fish accelerating in the water column, as seen in other teleosts.

The timing of various fast-start events was similar among groups of fish (Table 1). The duration of stage 1 showed a slight but nonsignificant tendency to decrease as the distance between the grid and the solid bottom increased. The fish accelerating from the grid lost contact after 112 ms, before the completion of stage 2 in 124 ms (Table 1).

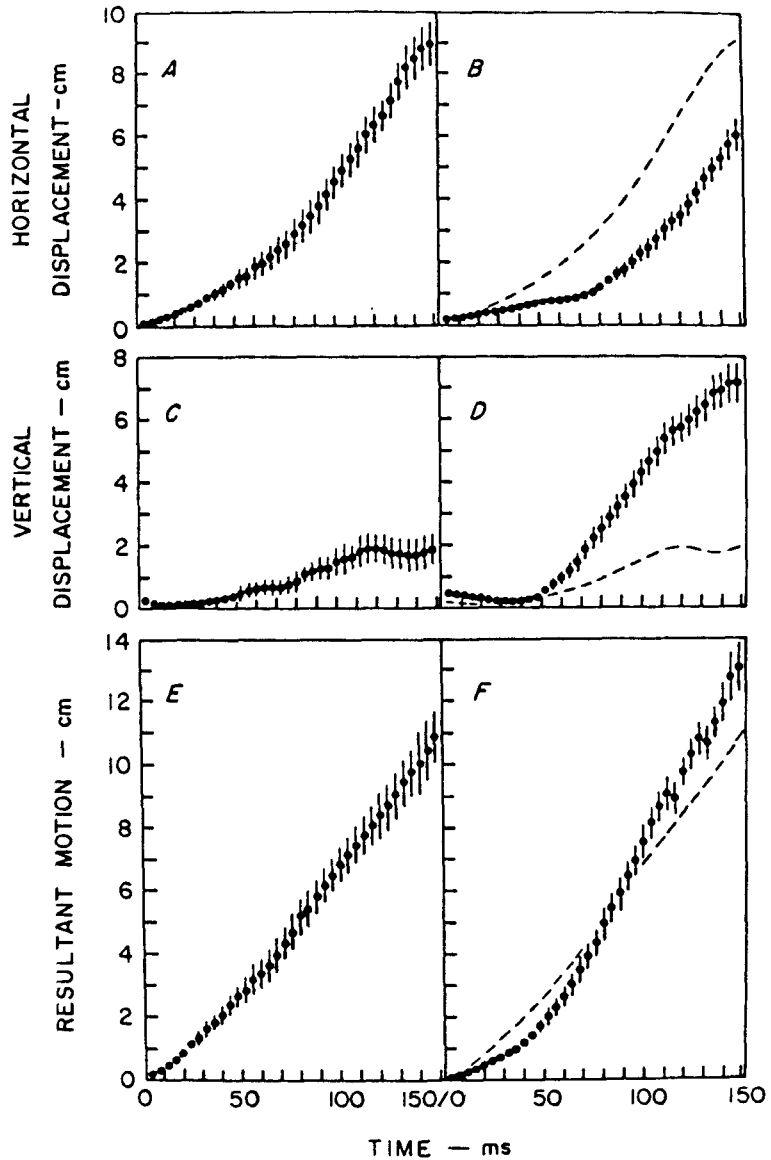
Fast-Start Performance

The distance between the solid bottom and the grid had no significant effect on vertical and horizontal distances traveled by the center of mass of speckled sanddabs during fast starts (Figure 2) including distances traveled after losing contact with the grid. This showed that no measurable

TABLE 1.—Results for the duration of fast-start events for *Citharichthys stigmaeus* accelerating from a grid at various distances above a solid bottom and accelerating in the water column. Mean \pm 2 SE are shown, $n = 10$.

Timing	Acceleration in the water column	Distance between the grid and the solid bottom (cm)				Combined data for acceleration from the grid
		0	1	3	6	
Duration of stage 1, ms	58 \pm 8	65 \pm 6	65 \pm 14	62 \pm 8	60 \pm 8	63 \pm 5
Duration of stages 1 plus 2, ms	105 \pm 12	136 \pm 18	118 \pm 13	149 \pm 40	113 \pm 9	124 \pm 7
Time to end of ground contact, ms	—	116 \pm 19	108 \pm 9	116 \pm 15	113 \pm 9	112 \pm 6

FIGURE 2.—Relationships between the distance traveled by the center of mass (the point about which propulsive forces act) and elapsed time during fast starts of *Citharichthys stigmaeus*. The motion of the center of mass was resolved into the distance traveled in the horizontal (A, B) and vertical (C, D) planes. These data were used to calculate the resultant distance traveled (E, F). Fast-start performance is shown for fish accelerating in the water column (A, C, E) and from the grid (B, D, F). The dotted lines in B, D, and F show the motions of the center of mass of fish accelerating in the water column from A, C, and E to facilitate comparison with fast starts from the grid. Vertical bars shown ± 2 SE.



hydrodynamic ground effect influenced speckled sanddab fast starts. All data for fish accelerating from the grid were therefore combined for subsequent analysis and for comparison with fish accelerating in the water column.

The performance of fish accelerating from the grid differed from that of fish accelerating in the water column. The differences were seen in horizontal and vertical motions and in the net (resultant) motion. In the horizontal plane, fish accelerating from the grid traveled 0.8 ± 0.2 cm in 63

ms at the end of stage 1, compared with 1.9 ± 0.4 cm in the same time for fish accelerating in the water column. By the end of stage 2 fish starting from the grid had moved forward 3.9 ± 0.9 cm in 124 ms. This was an improvement over stage 1, but still less than that of fish in the water column which moved forward 6.8 ± 0.9 cm in the same time. The small initial displacement of fish in contact with the grid was probably due to frictional interactions between the fish and the grid (Arnold and Weihs 1978). The normal force at the point of con-

tact would also have been augmented by recoil forces generated by the tail and head tending to displace the fish downwards.

The motion of the center of mass in the vertical plane also differed between speckled sanddabs accelerating from the grid and in the water column (Figure 2C, D). For fish accelerating from the grid there was little vertical movement during fast-start stage 1 because of the presence of that grid. During stage 2, however, the center of mass was accelerated vertically upwards moving 6.0 ± 2.4 cm in 124 ms. Fish accelerating in the water column showed little vertical motion, except that due to recoil (Figure 2C).

The resultant motion of the center of mass of the fish showed differences between acceleration in the water column and from the grid, but these differences were less marked than motions in the horizontal and vertical planes (Figure 2E, F). The increase in distance covered with time was initially greater for fish accelerating in the water column. They traveled a total of 3.7 ± 0.6 cm in 63 ms compared with 2.9 ± 0.4 cm for fish accelerating from the grid. However, once fish pushed against the grid in stage 2, performance improved. By the end of stage 2, they had traveled a cumulative distance of 10.2 ± 1.2 cm in 124 ms, greater than that of 8.7 ± 1.3 cm achieved by fish accelerating in the water column.

Velocities calculated for the center of mass reached maximum values close to the end of stage 2. Maximum values were significantly greater for fish accelerating from the grid compared with fish accelerating in the water column (Table 2). Mean acceleration rates would, of course, follow similar trends to velocities. Maximum acceleration rates only showed significantly improved performance for resultant motion of fish accelerating from the grid (Table 2).

TABLE 2.—Results of maximum acceleration rates and maximum velocities for *Citharichthys stigmaeus* accelerating from the grid and in the water column. Data (mean \pm 2 SE; $n = 10$) are shown for motion of the center of mass.

Item	Fast starts from the grid	Fast starts in the water column
Maximum acceleration rates, m/s^2 :		
Horizontal	37 \pm 7	48 \pm 10
Vertical	54 \pm 10	44 \pm 9
Resultant	66 \pm 12	46 \pm 12
Maximum velocities, m/s :		
Horizontal	66 \pm 11	92 \pm 10
Vertical	92 \pm 12	17 \pm 4
Resultant	104 \pm 17	76 \pm 14

DISCUSSION

These experiments show that the bottom (grid) does influence fast starts in speckled sanddabs. Fast starts from the bottom were associated with large amplitude motions that would normally cause substantial recoil of the center of mass because the bottom prevents that recoil. Motions of fish accelerating from bottom contact were predominantly vertical compared with horizontal motions of fish accelerating in the water column. The relative magnitude of vertical and horizontal displacements of sanddab accelerating from the grid are comparable with those observed in crayfish under similar circumstances (Webb 1979). For both speckled sanddab and crayfish the marked vertical motion is caused by prolonged contact between the body and the ground. Unfortunately, these large vertical displacements in speckled sanddabs preclude any significant hydrodynamic interaction with the ground after contact is lost.

Withers and Timko (1977) give a succinct explanation of this hydrodynamic ground effect, where the ground influences the flow, increasing lift (thrust) and decreasing drag. Hydrodynamic ground effect rapidly declines as the ratio, y/s , increases, where y is the gap between the surface generating thrust and the ground, and s is the span (width) of that surface. Blake (1979) found that 80-90% of the ground effect vanished by the time y/s reached unity in hovering mandarin fish. The mean maximum span of speckled sanddab, located at the center of mass, was 6.7 ± 0.2 cm. For this span, $y/s = 1$ after about 130 ms, 18 ms after the end of physical contact with the bottom (Figure 2D). The caudal fin had a maximum span of 2.4 ± 0.3 cm, and a value of $y/s = 1$ is reached within about 16 ms after the tail loses contact with the bottom (Figure 1A). Thus, the vertical acceleration rapidly lifts the speckled sanddab out of the hydrodynamic influence of the ground so that there is insufficient time for any interaction to affect performance. However, the absence of this effect during a fast start does not preclude hydrodynamic ground interactions from improving steady swimming close to the sea floor.

Thus, the observations on fast starts of speckled sanddab from the bottom show that a single kinematic pattern is used, which sustains bottom contact for most of a fast start, but which prevents development of any significant hydrodynamic ground effect. However, a direct push against a

solid substrate will always convert more muscle energy into body motion than working against a fluid. It therefore appears that speckled sanddab utilizes fast-start behavior that makes the greatest use of the available ground interaction options.

However, the interaction with the ground cannot be assumed to be adaptive before considering the question of advantages and disadvantages. For example, the small initial displacement of the center of mass of fish accelerating from the ground might be disadvantageous in some circumstances, such as escaping from predators. However, significant protection is achieved by camouflage and cryptic behavior in pleuronectiform fishes, rendering this contingency unlikely.

The influence of the bottom is clearly advantageous in the capture of elusive prey, a second behavior in which fast starts play a key role (Eaton and Bombardieri 1978; Webb and Skadsen 1980). Elusive prey, e.g., fish and crustacea, are common dietary items for pleuronectiform fishes in the families Psettodidae, Bothidae, and Pleuronectidae (Liem and Scott 1966; Norman 1966). The bottom eliminates recoil so that the fish can rapidly accelerate the head vertically (Figure 1). Continued rapid vertical acceleration is facilitated by prolonged bottom contact through the major acceleration period of a fast start. Bottom contact also results in the acquisition of a superior final speed that would be advantageous in a continued attack. The time taken to accelerate from the bottom and reach maximum speed could also be reduced by resting in sand in a curved U-shaped posture. This may occur since flatfish often dig into sand with the eyes and tail at the surface, but the body buried, implying a curved posture (Hobson 1979). Thus, the morphology and behavior of the benthic sanddab appear to be adaptive in improving fast-start performance, as well as for camouflage. Such advantages undoubtedly apply equally to other members of the pleuronectiformes and therefore provide an additional functional explanation of the unique flatfish body form and habits.

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