STATION-HOLDING BY THREE SPECIES OF BENTHIC FISHES

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Summary

Station-holding performance was determined on a smooth substratum and on a grid substratum for three species of benthic fishes differing in body shape, surface texture, density, friction coefficient and behavioural repertoire. The grid was made of wires parallel to the flow, which raised fish into the free stream. Limited observations were also made on the benthopelagic cod. Station-holding performance was evaluated at two speeds. The first was defined as the slip speed, above which activities such as swimming, fin-beating, body arching, body clamping and gripping the substratum were required to hold position on the substratum. The second was defined as the swim speed, when fish began swimming out of ground contact. Cod and lasher started swimming when they began slipping, so that slip and swim speeds were the same, averaging $6 \, \text{cm s}^{-1}$ for cod and $32 \, \text{cm s}^{-1}$ for lasher on the smooth surface. Body postures and fin-beating delayed swimming from a slip speed of about $20 \, \text{cm s}^{-1}$ to swim speeds of $47–58 \, \text{cm s}^{-1}$ for plaice and rays. The grid had relatively little effect on slip and swim speeds of plaice and rays. Lasher grasped the grid with their pectoral fins, increasing swim speeds to $55 \, \text{cm s}^{-1}$. Amputation of the posterior portion of the median fins of plaice reduced swim speeds on the smooth surface to $36 \, \text{cm s}^{-1}$. Amputation of the pectoral fins of lasher reduced the swim speed on the grid to $38 \, \text{cm s}^{-1}$.

Estimates of drag coefficients for fish were made using published data for blisters. These were used to determine lift coefficients and the effects of grasping the substratum on the friction coefficient. Comparison of lift coefficients of rays on the smooth substratum with those on the grid showed that flow beneath the body reduced lift. Amputation of the posterior of the median fins of plaice and the rarity of body posturing by plaice and rays on the grid showed that the major role of this station-holding behaviour was reduction of lift through induction of flow beneath the body. Lashers were able to hold station at speeds comparable to plaice and rays when they could utilize the small amount of surface structure of the grid to increase friction.

Benthic fishes tend to have either 'flattened' plaice- or ray-like forms with low drag coefficients but high lift coefficients, or more fusiform lasher-like forms with

high drag coefficients and low lift coefficients. High-lift forms use behaviour to reduce lift coefficients, whereas high-drag forms use behaviour to increase friction.

Introduction

Animals benefit from currents bringing food, olfactory stimuli and mates, and providing economical transport for migration and dispersal. Currents also are potentially disadvantageous as they tend to displace organisms from the substratum where the non-transport benefits can be realized. Active animals, such as fish, can hold position by swimming, but this is energetically expensive. Furthermore, many fish are unable to sustain speeds comparable to normal stream flows (Hynes, 1970; Beamish, 1978; Probst *et al.* 1984). Therefore, exploitation of currents usually requires that organisms have flow refuges adjacent to, but out of, the mainstream.

Organisms may escape flow by burrowing in soft substrata when currents are slow, or by hiding in gaps between boulders and rocks left by high currents. The greatest difficulties occur when these options are not available. Then, the free-stream speed up to which animals hold station depends on the magnitude of forces promoting and preventing slippage (Stuart, 1958; Arnold & Weihs, 1978; Blake, 1985; Denny, 1988). Arnold & Weihs (1978) have described how body shape and behaviour of plaice, *Pleuronectes platessa*, can affect lift and drag forces that, respectively, raise a fish from the bottom and displace it downstream. The present work builds on this study. The purpose is to evaluate the basic mechanisms available for fish holding station on smooth surfaces and those with little surface structure by addressing three questions. (a) How do the physical properties of the body vary among benthic species? (b) To what extent can individual fish modify these basic physical properties? (c) How does the ability to hold station vary among benthic species? Three benthic species with different body forms, surface textures and behavioural repertoires were used. Fin amputations were used with two species to modify station-holding behaviour believed to effect the mechanics of substratum interactions.

Materials and methods

Fish

Observations concentrated on three benthic species, plaice (*Pleuronectes platessa*), thornback ray (*Raja clavata*) and father lasher (*Myoxocephalus scorpius*). Observations were also made on a benthopelagic species, the cod (*Gadus morhua*). Since the station-holding ability of cod in ground contact was so small, observations on this species were limited. All fish were caught near Lowestoft (England) using beam trawls, and were held in the laboratory for 4–6 weeks before the start of experiments. The fish were held in 1200-l tanks, continuously aerated and flushed with filtered sea water. Fish were fed on chopped lugworm, mackerel and herring.

Station-holding performance was measured for plaice and lasher before and after amputation of the fins used for station-holding. These fins were the posterior half of the dorsal and anal fins of plaice and the pectoral fins of lasher. Fish were anaesthetized in $1\,ml\,l^{-1}$ phenoxyethanol before fin amputation. Fish recovered in sea water before being returned to the holding tank. They were retested 3–7 days later, when they had recovered and fin rays and web were beginning to grow back.

Apparatus

Station-holding performance was observed in a flume, described in detail by Arnold (1969a). Briefly, the flume was constructed from 12·5 mm thick Perspex. It was approximately 6 m long, with a 0·3 m × 0·3 m square cross-section. Water entered *via* a contraction cone, so that the flow profile was rectilinear at the entry to the flume. The first 1·8 m of the flume was an entry section which was followed by a 1·8 m observation section. The entry section ensured that fish were not exposed to large changes in shear stresses due to rapid growth of the boundary layer that occurs over the upstream region of a surface (Schlichting, 1968). The observation section was delineated by nylon mesh screen and clear Perspex boats floated on the surface to eliminate surface waves. The final 1·8 m of the flume terminated in a gate, the height of which was adjusted to regulate flow velocity. Free-stream flow velocity was continuously monitored using a MINFLOW meter 15 cm above the solid bottom immediately upstream of the observation section.

Fish holding station were observed on a smooth (Perspex) substratum and a grid. Cod were only observed on the smooth substratum. The grid extended the length of the observation section and lifted fish 50 mm above the solid bottom of the flume, and out of the boundary layer of that bottom. The grid consisted of an aluminium frame (10 mm × 10 mm × 2 m), with 6·25 mm diameter cross-pieces at each end. The latter were covered with Tygon tubing and streamlined. Stainless-steel wires (0·01 mm diameter) were strung at 10 mm intervals along the cross-pieces, and held under tension by turnbuckles at the downstream end of the grid. Thus, the wires were oriented parallel to the flow, preventing fish from hooking onto them.

Flow profiles were measured over the smooth substratum and the grid using an array of four pitot-static tubes. The array was mounted on a heavy stand, with a screw raising and lowering the tubes to sample pressures throughout the water column. Pressures were measured at 5 mm intervals from the flume bottom across the flow at the centre of the flume, as described by Arnold & Weihs (1978) and Cook (1985). Inclined manometers containing low-density fluid and stabilizing pots provided pressure amplification of up to 50 times. Flow profiles were measured at five free-stream velocities spanning the range at which fish were tested.

An example of boundary layer flow profiles is given in Fig. 1. Flow over the smooth surface showed the normal logarithmic increase in velocity with height above the bottom (Schlichting, 1968). The grid eliminated the no-slip condition at its surface. However, flow was retarded by up to 20 % by the drag of the wires.
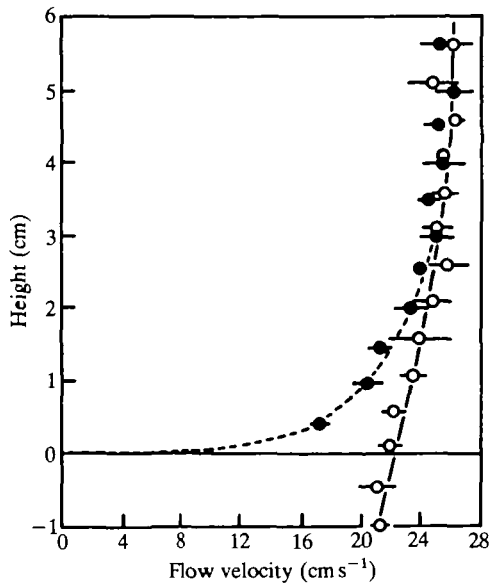
Fig. 1. An example of flow profiles over the smooth substratum (dotted line and solid symbols) and over the grid (solid line and open symbols). Lines are smoothed curves calculated from velocity measurements determined using pitot-static tubes at various heights from the substratum surface. Symbols are mean with horizontal bars showing one standard deviation.

Experimental procedure

Fish were placed in the observation section and left overnight at a free-stream velocity of 5–10 cm s^{-1}. The following morning, the flow velocity was increased in increments of 5–10 cm s^{-1} every 10 min. Slipping, body posture, fin-beating and swimming were recorded. Frequency of fin movements was measured with a stopwatch for plaice and rays. The experiment terminated after fish began continuously swimming out of ground contact and were unable to swim off the downstream grid delineating the observation section. Test temperature was 15 °C. Sea water density was 1·025 g cm^{-3}.

At the end of an experiment, static friction coefficients were measured for plaice, rays and lashers. Fish were anaesthetized (1 ml l^{-1} phenoxyethanol) and placed on a Perspex sheet or grid in sea water from the flume. The fish-head end of the Perspex sheet or grid was slowly raised by a thread attached to a windlass (6·3 mm diameter). The friction coefficient was calculated from the average of two measurements of the angle of inclination of the plate at which the fish first slipped (Arnold & Weihs, 1978).

Post mortem measurements were made of planform, total length, mass and weight in water. The surface area of the body was determined from the sum of the circumferences of the body, measured using threads, at 1 cm intervals along the body length. Fin areas were measured from tracings of extended fins using a
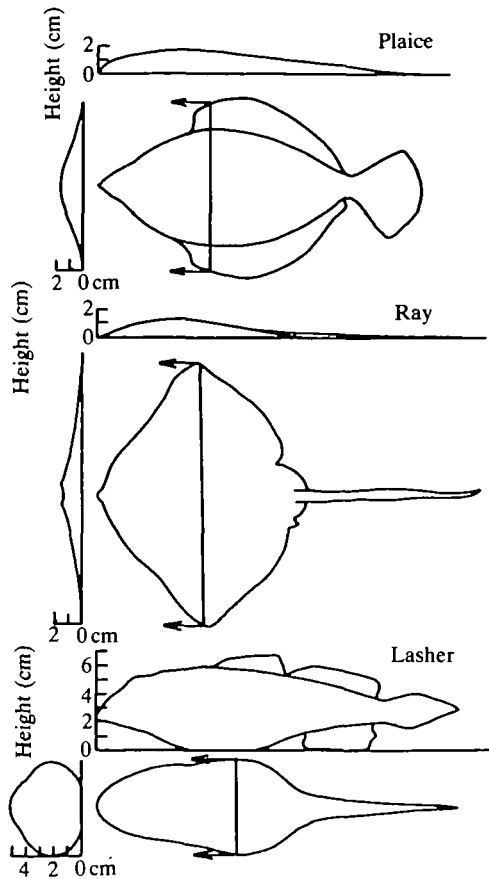
Fig. 2. Planforms, cross-sections and longitudinal sections of plaice, rays and lashers.

planimeter. The longitudinal and cross-sectional body shapes were measured by using a vertical probe, raised and lowered on a screw. The probe was lowered to a point on the body, and the height on a scale was recorded. This was repeated at 5 mm intervals both along and across the body. The cross-sectional shape of lasher was also observed from sections of frozen material (Fig. 2 and Table 1). Cod were $25 \cdot 1 \pm 1 \cdot 4$ cm in total length, and $128 \cdot 6 \pm 23 \cdot 4$ g in mass.

Results

Station-holding behaviour on the smooth substratum

At low free-stream velocities, some plaice, rays and lashers were not oriented to the flow (Fig. 3). The longitudinal body axis of these fish subtended angles up to 180° to the flow. Cod oriented the longitudinal body axis parallel to the flow at all current velocities.

As flow velocity increased, non-oriented fish slipped and then oriented to the flow (Arnold, 1969b; Arnold & Weihs, 1978). Lashers held their pectoral fins

extended between the substratum and the body. The anterior ventral portion of the fin contacted the substratum, and typically extended forward. The posterior dorsal portion of the fin was in contact with the lateral body surface. Therefore, the pectoral fins streamlined the anterior of the body (Hoerner, 1965). Five of 11 cod held station with their pectoral fins and posterior body in contact with the

Table 1. *Morphometric data for the three species of benthic fish used in experiments*

|	Plaice	Ray	Lasher
Total length (cm)	26·4 ± 0·07	27·2 ± 3·6	24·1 ± 2·5
Disc length (cm)		14·8 ± 2·2	
Maximum width of body and fins (cm)	14·4 ± 0·4	18·6 ± 2·9	
Maximum body width without fins (cm)	10·0 ± 0·4		6·8 ± 0·2
Maximum body height (cm)	1·7 ± 0·2	1·5 ± 0·1	5·8 ± 0·4
Total mass (g)	184·93 ± 33·56	108·51 ± 34·51	311·85 ± 50·75
Weight in water (g)	8·345 ± 1·456	4·014 ± 1·255	6·696 ± 2·185
Density (g cm^{-3})	1·074 ± 0·002	1·066 ± 0·008	1·047 ± 0·005
Total wetted surface area (cm^2)	469 ± 30	352 ± 96	365 ± 45
Body plus fin frontal surface area (cm^2)	13·6 ± 2·5	11·3 ± 1·4	28·9 ± 3·1
Body frontal surface area (cm^2)			15·5 ± 3·1
Area in contact with the bottom surface (cm^2)	232 ± 15	169 ± 45	31 ± 4
Passive friction coefficients of anaesthetized fish on			
Smooth substratum	0·21 ± 0·056	0·36 ± 0·10	0·69 ± 0·24
Grid substratum	0·099 ± 0·03	0·48 ± 0·092	0·35 ± 0·12

Values are means ± s.e., $N = 7$.
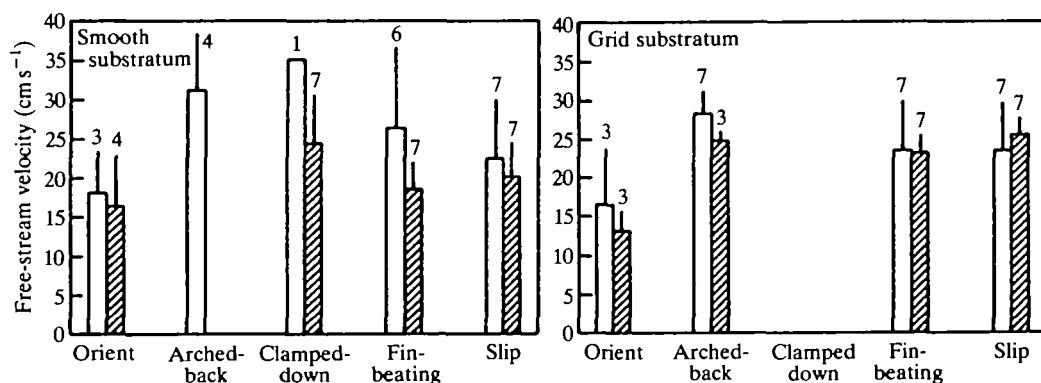
Fig. 3. Free-stream velocities at which various types of station-holding behaviour were first seen for plaice (open boxes) and rays (shaded boxes). Vertical bars are ±2 s.e. The number of fish (out of 7) showing each behaviour is shown.

substratum, similar to the 'parr posture' described for Atlantic salmon, *Salmo salar* (P. W. Webb, G. P. Arnold & B. H. Holford, in preparation). Cod, plaice, rays and lashers remained oriented, with no change in body posture until they began to slip downstream consistently.

Once fish began slipping downstream, behaviour such as swimming out of ground (substratum) contact, various body postures and/or fin-beating were required to hold station (Fig. 3). Following Arnold & Weihs (1978), I define the minimum free-stream current velocity at which slipping is unavoidable without the intervention of such behaviour as the *slip speed*, u_{slip}, with $u_{slip,smooth}$ being the slip speed of fish on the smooth substratum.

Six of 11 cod swam out of ground contact at all speeds studied. Others began swimming using body and caudal fin motions as soon as they slipped. Lashers slipped downstream for several body lengths, then swam upstream using the body and caudal fin and attempted to resettle on the substratum. Usually they slipped downstream again, and had to swim back upstream. This behaviour merged into continuous swimming out of ground contact. Therefore, once lashers that were oriented began slipping, swimming out of ground contact was required to maintain position relative to the substratum.

In contrast, plaice and rays delayed the onset of swimming out of ground contact using body postures and fin-beating behaviour as described by Arnold (1969b), Arnold & Weihs (1978) and Cook (1985). This behaviour occurred as soon as fish began slipping consistently, and hence was first seen at speeds not statistically different (*t*-test; $P > 0.05$) from the slip speed (Fig. 3). Behaviour varied among individuals. Some plaice showed the *arched-back posture* and one plaice and all the rays showed the *clamped-down posture* (Arnold & Weihs, 1978). In both postures, the middle portion of the body was lifted from the bottom. In the arched-back posture the fins were raised but in the clamped-down posture the fins were pressed on the substratum. Raising the posterior margin of the median fins was also seen in plaice and rays (Cook, 1985), presumably done to generate negative lift. This behaviour was succeeded by fin-beating at higher free-stream velocities.

Posterior fin-beating (Arnold & Weihs, 1978) was the most prevalent station-holding behaviour above u_{slip}, sometimes occurring in conjunction with the arched-back posture. A wave of 3–15 beats was passed along the posterior one-third to half of one or both of the median fins of plaice (Arnold & Weihs, 1978) and along the posterior half of the pectoral fins of rays. Wave frequencies were variable but there was a significant increase ($P < 0.05$) in plaice from 1 Hz at $20\,\mathrm{cm\,s^{-1}}$ to about $1.5\,\mathrm{Hz}$ at $50\,\mathrm{cm\,s^{-1}}$. Frequencies for rays covered the same range, but there was no significant increase with speed ($P \gg 0.05$). The proportion of time when posterior fin-beating occurred appeared to increase with flow rate, but no significant trend was found ($P \gg 0.05$).

As flow velocity increased, plaice and rays again began slipping downstream. Initially, the fish swam back upstream and resettled, as did the lashers. Eventually, resettling was no longer possible, and fish began to swim continuously out of ground contact.

I define the minimum free-stream current velocity at which fish swim out of ground contact as the *swim speed*, u_{swim}, with $u_{swim,smooth}$ being the swim speed of fish over the smooth substratum. Saunders (1965) defined the speed at which salmon parr began swimming out of ground contact as the critical speed. Since both u_{slip} and u_{swim} could be considered critical for different reasons, I prefer not to use Saunders' term.

For plaice and rays, $u_{slip,smooth}$ was similar at about $20\,cm\,s^{-1}$. Fin-beating and body posturing resulted in swimming being delayed to $u_{swim,smooth}$ at $47\,cm\,s^{-1}$ for rays and $58\,cm\,s^{-1}$ for plaice, but this difference was not quite significant (Fig. 4; t-test, $P = 0.05$). For lashers and cod, $u_{slip,smooth}$ and $u_{swim,smooth}$ occurred at the same speed. This speed was $32\,cm\,s^{-1}$ for lasher. The $u_{swim,smooth}$ of cod, $6\,cm\,s^{-1}$, was significantly lower than $u_{slip,smooth}$ and $u_{swim,smooth}$ of the other species (Fig. 4).

Amputation of the median fins of plaice and the pectoral fins of lasher had no effect on $u_{slip,smooth}$ and $u_{swim,smooth}$, respectively. However, $u_{swim,smooth}$ of plaice was significantly reduced (Fig. 4). Plaice also showed fin-beating over the anterior portion of the median fins which remained after amputation. This portion of the fin was not used for fin-beating by intact plaice. Fin-beating of the anterior of the fin appeared to be less vigorous and smaller in amplitude than that of the posterior of intact fins.
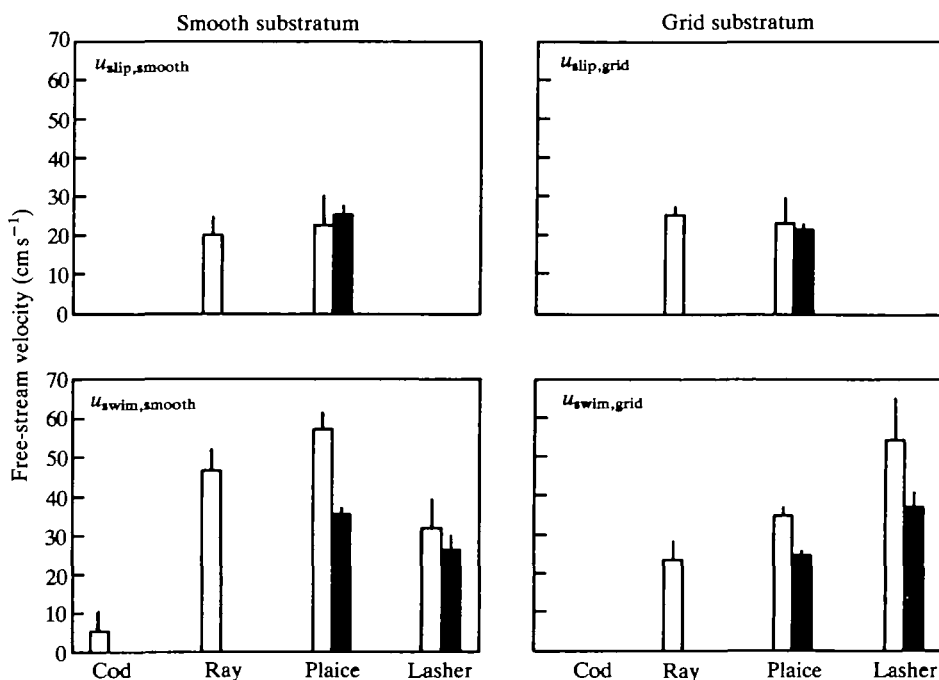

Fig. 4. Slip and swim speeds of fish on the smooth substratum and on the grid. Open boxes show performance of intact fish. Stippled boxes show performance of plaice and lashers following fin amputation.

Station-holding behaviour on the grid substratum

There were few differences in behaviour between fish on the smooth substratum and on the grid. Rays and plaice showed posterior fin-beating on the grid, but only at current velocities close to $u_{slip,grid}$, where the subscript 'grid' denotes station-holding performance measures for fish on the grid. For most of the speed range, therefore, fin-beating was essentially absent for rays and plaice on the grid. Lasher and plaice projected the finger-like distal portion of their pectoral and median fins, respectively, through the grid and grasped the wires.

The $u_{slip,grid}$ of rays and plaice was about 24 cm s^{-1}. However, $u_{swim,grid}$ of plaice, 35 cm s^{-1}, was significantly greater ($P > 0.05$; Fig. 4) than that of 24 cm s^{-1} for rays. The $u_{slip,grid}$ and $u_{swim,grid}$ of lasher were again equivalent at 55 cm s^{-1}, exceeding $u_{swim,grid}$ of plaice and rays (Fig. 4).

Amputation of the posterior portion of the median fins had no significant effect on $u_{slip,grid}$ of plaice, but $u_{swim,grid}$ was reduced significantly ($P < 0.05$) for both plaice and lasher. Following amputation of the posterior portion of the median fins of plaice, the remaining anterior portion attempted to grasp the grid wires, as had the posterior fin portion of intact fish.

Discussion

The questions addressed here are as follows. (a) How do the physical properties of the body vary among benthic species? (b) To what extent can individual fish modify these basic physical properties? (c) How does the ability to hold station vary among benthic species? Answering these questions requires estimates of the variables affecting station holding.

Theoretical considerations

The factors affecting station-holding are defined by the balance of forces promoting and resisting displacement. The equation for the force balance can be rearranged to isolate dimensionless coefficients for drag, lift and friction, equating them to a dimensionless product group combining body and performance measurements (Arnold & Weihs, 1978).

Assuming horizontal rectilinear flow, forces in the plane of the flow are friction, F, opposing drag, D:

$$F = \mu(W_o g - L) = D, \tag{1}$$

where μ is the friction coefficient, W_o is the weight of the fish in water, g is the acceleration due to gravity, and L is the lift.

$$L = 0.5\rho_w A_f u^2 C_{Lo}, \tag{2}$$

$$D = 0.5\rho_w A_f u^2 C_{Do}, \tag{3}$$

where A_f is the frontal area, C_{Do} is the frontal drag coefficient, C_{Lo} is the frontal lift coefficient, u is the free-stream velocity and ρ_w is the density of water.

Substituting for L and D from equations 2 and 3 into equation 1, and rearranging, Arnold & Weihs (1978) obtained:

$$\frac{2W_o g}{\rho_w A_f u^2} = C_{Lo} + \frac{C_{Do}}{\mu}. \tag{4}$$

The descriptive variables for the body in the product group $2W_o g/\rho_w A_f u^2$ on the left of equation 4 are W_o and A_f. These are essentially constants, although W_o, being a function of body volume and fish density, can be modified by changes in body composition (Bone & Marshall, 1982). Such changes are usually slow, except for physostomatous fish expelling air from the gas bladder (Gee, 1983).

The product group on the left includes u, so that $2W_o g/\rho_w A_f u^2$ will take a maximum value at u_{slip} depending on C_{Lo}, C_{Do} and μ for a given body shape, and a lower value at u_{swim}, reflecting the maximum modification of these coefficients by behaviour. Thus the magnitude of $2W_o g/\rho_w A_f u^2$ at u_{slip} and u_{swim} (Table 2) is the critical metric needed for comparison of performance among species (Arnold & Weihs, 1978).

Estimation of drag and lift coefficients on the smooth substratum

Unfortunately, C_{Do} and C_{Lo} are both unknown for fish, but their magnitude must be estimated. This was recognized as a major difficulty in the analysis of station-holding performance by Arnold & Weihs (1978). Direct measurement on live fish would be extremely difficult, and cast models do not faithfully replicate fish properties (Arnold & Weihs, 1978). Arnold & Weihs approached the problem of unknown C_{Do} and C_{Lo} for plaice by recognizing that individuals of this species on a smooth substratum have the same general body form as blisters designed for farings on aircraft and submersibles. I followed their methods by using C_{Do} data for blisters to set probable C_{Do} values. C_{Lo} is then obtained from equation 4, using $2W_o g/\rho_w A_f u^2$ at u_{slip} and u_{swim} (Table 2) and μ (Table 1).

Plaice have many features of blisters designed to have minimum drag (Arnold & Weihs, 1978). The minimum C_{Do} for a streamlined blister on a flat surface, and with fineness ratio, l/H, greater than 10, is given by (Hoerner, 1965):

$$C_{Do} = 0.5C_{Df}(l/H), \tag{5}$$

where l is total length, H is height and C_{Df} is the friction drag coefficient based on wetted surface area. For plaice, with l/H of 15·5, $C_{D,f}$ is 0·0055, and C_{Do} is 0·04. Arnold & Weihs (1978) considered that the eyes, operculum, etc. would elevate C_{Do} by a factor of 2–0·08. Using this value for C_{Do} gives a value of 2 for C_{Lo} for the plaice used here (Table 2 and Fig. 5).

The fineness ratio of the body disk of the rays was 10, suggesting that C_{Do} on the smooth surface would be similar to that for plaice. However, rays are not as well streamlined as plaice-like blisters. The body cross-section is. more concave dorsally, and there are rows of large scales along the apex of the body (Fig. 2). The tail does not provide a smooth transition to the substratum. The effect of these factors on C_{Do} is not clear, although the lack of downstream body faring would

Table 2. *Summary of estimated drag coefficients, C_{Do}, and derived lift coefficients, C_{Lo}, determined from the product group $2W_og/\rho_w A_f u^2$ and passive friction coefficients μ*

Test situation	$2W_og/\rho_w A_f u^2$	C_{Do}	μ	C_{Lo}
At slip speeds for fish on smooth substratum				
Ray	1·67	0·1	0·36	1·39
Intact plaice	2·32	0·08	0·21	1·94
Plaice with median fins amputated	1·85	0·08	0·21	1·47
At swim speeds for fish on smooth substratum				
Cod				
Ray	0·31	0·1	0·36	0·032
Intact plaice	0·36	0·08	0·21	−0·03
Plaice with median fins amputated	0·92	0·08	0·21	0·54
Lasher	0·43	0·12	0·69	0·25
Lasher with pectoral fins amputated	0·63	0·12	0·69	0·45
At slip speeds for fish on grid substratum				
Ray	1·05	0·45	0·48	0·11
Intact plaice	2·15	0·45	0·099	−2·4
Plaice with median fins amputated	2·45	0·45	0·099	−2·1
At swim speeds for fish on grid substratum				
Ray	1·19	0·45	0·48	0·25
Intact plaice	0·94	0·45	0·099	−3·6
Plaice with median fins amputated	1·88	0·45	0·099	−2·7
Lasher	0·18	0·12	0·35	−0·16
Lasher with pectoral fins amputated	0·31	0·12	0·35	−0·031

increase drag by about 5 % compared with a plaice-like shape (Hoerner, 1965). I assume C_{Do} to be about 0·1, which would require C_{Lo} to be 1·4 for the observed μ on the smooth substratum (Table 2 and Fig. 5).

Low-drag blisters with a fineness ratio of 4·2, the value for lasher, on a solid planar surface, have C_{Do} 70 % larger than those of plaice-shaped blisters (Hoerner, 1965). Lashers, however, are least amenable to modelling as blisters. Thus, the body is not semi-elliptical in cross-section, but is rounded so that the maximum width is raised above the substratum. Flow compression beneath such a body could contribute negative lift. In contrast, the trailing edge is vertical, and the body is not fared smoothly with the substratum, which would increase drag and reduce lift. Therefore, I assume that C_{Do} of lasher on the smooth substratum is about twice that of plaice, and I assign C_{Do} a value of 0·16. At $u_{swim,smooth}$, and μ of 0·69, C_{Lo} of lasher would be 0·5 on the smooth substratum (Table 2 and Fig. 5).
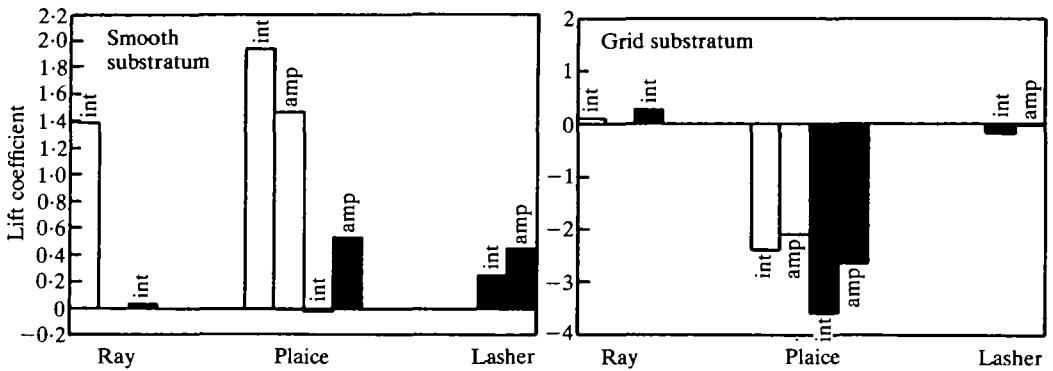
Fig. 5. Lift coefficients estimated for rays, plaice and lashers on the smooth sub-stratum and on the grid. Open squares show values at slip speeds, and stippled boxes show values at swim speeds. Intact fish are identified by int, while amp denotes plaice and lashers following fin amputation.

Estimation of drag and lift coefficients on the grid substratum

Water flowed on all sides of fish on the grid (Fig. 1), so that drag coefficients of fish will not be the same as on the smooth substratum. The appropriate C_{Do} will be similar to that of a fish in the free stream.

The flume used for these experiments was designed to give laminar flow when minimum C_{Df} is given by (Hoerner, 1965):

$$C_{Df} = 1.32Re^{-0.5}, \tag{6}$$

where Re is Reynolds number.

Converting from wetted to frontal surface area (Table 1), and again assuming that nares, eyes etc. double the drag (Arnold & Weihs, 1978), C_{Do} is estimated to be 0.4 for both plaice and rays, and 0.12 for lasher. These estimates lead to a reduction of C_{Lo} close to zero for rays on the grid.

Modification of the friction coefficient

Anomalous negative values for C_{Lo} were calculated for plaice at $u_{slip,grid}$ and for plaice and lasher at $u_{swim,grid}$ (Table 2 and Fig. 5). This result is improbable. The bodies of all the fish were cambered, and the flow velocity over the substratum surface must be lower than that over the upper surface (Fig. 1). Plaice and lasher were observed to grasp the grid with their fins, and the apparent elevation of C_{Lo} would be explained by an increase in μ due to this behaviour.

A maximum estimate of such an increase in μ can be obtained by recognizing that C_{Lo} is virtually reduced to zero for rays on the grid which lacked behaviour to interact with the wires and affect μ. Assuming C_{Lo} of plaice and lasher, like that of rays, approaches zero and C_{Do} is unchanged, then, using the values for $2W_o g/\rho_w A_f \mu^2$ at $u_{swim,grid}$, μ is estimated to be of the order of 0.48 for plaice and 0.80 for lasher. These are increases of 4.8-fold and 2.4-fold, respectively, compared with the measured values for anaesthetized fish on the grid. Although

plaice appear to increase μ by a greater *factor* than lashers, the absolute value of μ for lashers remains larger than that for plaice.

Amputation of the pectoral fins of lasher reduced $u_{\text{swim,grid}}$. Making the same assumptions on C_{Lo}, μ would be reduced to 0·39, similar to that of 0·35 for anaesthetized fish on the grid. The amputation of the posterior portion of the median fins of plaice also reduced $u_{\text{swim,grid}}$, implying a reduction of μ to 0·24. This is larger than μ for the anaesthetized fish. However, plaice continued to grasp the wires with the remaining anterior portion of the median fins.

Consequences of errors in drag and lift coefficient estimates

The analysis above provides estimates of C_{Lo}, C_{Do} and μ for fish that can be used to examine how different species use various mechanisms for station-holding. All further discussion, therefore, hinges on the validity of these estimates. Fortunately, the absolute values of C_{Do} and C_{Lo} are less important than their relative magnitudes in evaluating mechanisms used by various species.

The magnitudes of C_{Do} and, hence, derived values for C_{Lo} and/or μ, are critical for arguments relating to (a) body characteristics at $u_{\text{slip,smooth}}$; (b) consequences to lift for rays at $u_{\text{slip,smooth}}$ and $u_{\text{slip,grid}}$; (c) reduction of lift by fin-beating up to u_{swim}; and (d) modification of μ.

First, C_{Do} is postulated to be larger for plaice and rays than for lasher on smooth substratum, leading to high lift coefficients for plaice and rays, but low lift coefficients for lasher. The same conclusions concerning lift will be obtained irrespective of C_{Do} values, providing these are smaller for plaice and rays than for lasher. Measurements on blisters (Hoerner, 1965) clearly show that C_{Do} of shapes flattened parallel to the flow, as are plaice and rays, have very much lower drag coefficients than lashers. There are no obvious factors that would lead to any other conclusion.

Second, differences in C_{Lo} of rays on the smooth substratum and on the grid are used to argue that flow beneath the body results in a large reduction in lift, as assumed by Arnold & Weihs (1978). This conclusion rests on the assumption that C_{Do} is substantially higher for rays on the grid than on the smooth substratum. Again, it is highly improbable that C_{Do} would not be elevated on the grid. The wetted surface area of rays (and plaice) is almost doubled for fish on the grid (Table 1). Since C_{Do} is based on constant frontal area, the increase in wetted surface area must elevate C_{Do}, unless the flow velocity at the grid surface is zero. This is not the case (Fig. 1).

The same situation applies to the conclusion that C_{Do}, and hence μ, is elevated by plaice and lashers on the grid. C_{Lo} appears to be negative, which is improbable, but the conclusion rests on the relatively higher C_{Do}, and hence lower C_{Lo}, of plaice and lasher on the grid compared to values for these fish on the smooth surface.

Third, fin-beating is postulated to be a major mechanism inducing flow beneath the body, reducing lift and increasing station-holding performance (Arnold & Weihs, 1978). Calculations here suggest that fin-beating reduces C_{Lo} at

$u_{swim,smooth}$, an effect partially eliminated for plaice by median fin amputation. However, fin-beating must also produce thrust since this behaviour accelerates water caudally beneath the body. Therefore, the estimates of C_{Do} are highly likely to overestimate the vector difference between drag and thrust, and the major role of fin-beating might be thrust production not lift reduction.

The simplest evidence against a significant role of thrust generation for fin-beating comes from the virtual elimination of this behaviour by plaice and rays on the grid. Thrust generation would be equally effective to improve station-holding performance on both the smooth substratum and the grid. However, behaviour leading to lift reduction will only be effective on the smooth substratum. Therefore, absence of fin-beating on the grid argues that this behaviour, and presumably body posturing, is critical in lift reduction and serves only a minor role in thrust generation.

In addition, thrust cannot exceed drag. This would cause the fish to accelerate, which did not occur until fish swam clear of the ground. Therefore, the thrust due to fin-beating could not exceed a maximum value equal to drag at $u_{swim,smooth}$. Thus, thrust production would be equivalent to a reduction in C_{Do}, with a limiting value of zero for C_{Do}/μ. At this limiting value, C_{Lo} takes values of $2W_o g/\rho_w A_f u^2$. Then C_{Lo} would be about 1·9 for intact plaice at $u_{slip,smooth}$, reducing to 0·4 at $u_{swim,smooth}$. Therefore, lift reduction due to fin-induced flow beneath the body is still seen.

However, C_{Do} may be elevated by body movements (Lighthill, 1971), with thrust too small to offset the increase in drag. However, such an increase in C_{Do} would increase C_{Do}/μ, decreasing C_{Lo} even further at $u_{swim,smooth}$. Since fin-beating does not occur at u_{slip}, this would increase the subsequent reduction in C_{Lo} due to fin-beating.

These arguments show that the general conclusions concerning C_{Do}, C_{Lo} and μ remain, even if absolute values are in error.

Effects of physical characteristics of the body on station-holding

The inability of cod to hold station shows that body characteristics, body postures, fin-beating behaviour and substratum-grasping behaviour of benthic fish are essential for resisting downstream displacement in currents. The first line of defence for such benthic fish is the basic properties of the body, since once established they require little further energy to operate. Consideration of the shapes of benthic forms (e.g. Bone & Marshall, 1982) shows there are two common patterns: (a) the 'flattened' form, either compressed as in plaice or depressed as in rays, and (b) a less depressed, more fusiform shape typical of cottids, including lashers. The C_{Do} for plaice and rays is smaller than for lasher, but C_{Lo} is smaller for lasher than for plaice/rays. This suggests two modal forms with high-lift/low-drag or low-lift/high-drag.

An inverse correlation between C_{Lo} and C_{Do} is probably inescapable. If a fish is to conserve its volume, and hence space for muscle, viscera, gonads, etc. (Vogel, 1981), body flattening parallel to the flow to minimize drag must be associated with

extension of the body normal to the flow. The concomitant increased planform area will increase lift and C_{Lo}.

W_o and μ may also vary for either a low-drag/high-lift or high-drag/low-lift form. As noted above, W_o reflects body density, ρ_b. Increased ρ_b and μ both improve station-holding performance, since high density will result in a large W_o which, with high μ, increases u_{slip} and u_{swim}. Body density of plaice was larger than that of rays (Table 1). Given the similarity of C_{Lo} and C_{Do}, this should promote station-holding. However, the friction coefficient of rays, with placoid scales giving a rough surface texture, was larger than for plaice. Presumably, similar variation is possible for more fusiform morphologies, but insufficient species were tested here.

Ideally, a benthic fish exposed to a current should increase both ρ_b and μ. However, for the species tested, ρ_b and μ appear to be inversely related. This probably reflects anatomical constraints in the lineages from which species were selected. The skeleton of elasmobranchs is cartilaginous, compared with bone in actinopterygians. Although cartilage may be reinforced by inorganic deposits, its density is lower than that of bone (Bone & Marshall, 1982). Therefore, cartilage in elasmobranchs is probably a contributing factor preventing them from achieving high density.

However, elasmobranch placoid scales give high surface roughness and larger μ (Table 1). Perhaps it is difficult to make mucus-covered cycloid scales very rough. A major exception occurs among the loricariid catfishes, with tooth-like projections through their armour (Berra, 1981). These fish forage in fast-flowing streams on algal mats where such projections would be especially effective for increasing μ by catching in the mat.

Surface roughness from scales is not essential for large μ. The soft scaleless belly of lasher had a larger μ than rays and plaice on the smooth substratum. Perhaps the soft, flaccid belly was better able to mesh with minute irregularities in the substratum.

In general, it appears that μ can be affected in many ways. More observations on mechanisms affecting μ of benthic fishes are desirable before generalizations can be made.

Behavioural modification of C_{Lo} and μ

Arnold & Weihs (1978) postulated that behavioural reduction of C_{Lo} was an important function of behaviour for benthic fish. The principle that lift reduction follows from flow induction over the substratum surface of the body is confirmed here. Furthermore, the pattern of fin-beating behaviour of plaice and rays, and the effects of fin amputation on plaice performance, show their major role in inducing the requisite flow, as Arnold & Weihs (1978) postulated. For plaice and rays, $u_{swim,smooth}$ is about 2·4 times $u_{slip,smooth}$. However, resistance increases with u^2, so that the difference in resistive forces is about sixfold. Thus, posturing and fin-beating are very effective in delaying the onset of free swimming. These activities
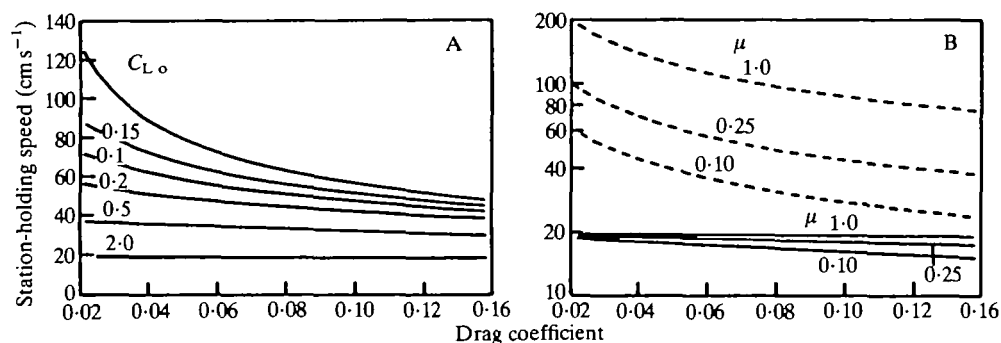
Fig. 6. Interactions between drag, lift and friction coefficients for idealized benthic fish on smooth substratum. (A) Relationship between speed to which a fish can hold station and drag coefficient for a range of lift coefficients. $W_o = 6$ g; $A_f = 15$ cm^2; $\mu = 0.4$. (B) Relationship between speed to which a fish can hold station (note the logarithmic scale) and friction coefficient. The dotted curves are for low lift coefficient, $C_{Lo} = 0$. The solid curves are for $C_{Lo} = 2$. $W_o = 6$ g; $A_f = 15$ cm^2.

will, of course, expend energy, but they can be sustained for long periods whereas swimming fish would be quickly exhausted.

Plaice and lasher, but not rays, were also observed to grasp the wires of the grid substratum, probably increasing μ by a factor of 2 to 5. The thick, smooth-edged fins of rays apparently prevented these fish from grasping the grid. Grasping substratum structure is probably most effective when fins have a finger-like margin, which does not occur among elasmobranchs. The cartilage skeleton may be unable to generate large enough bending moments for an elasmobranch fin to grasp the substratum.

Comparison of station-holding mechanisms among species

The general importance to benthic fish of lift, weight and friction modifications shown by the species studied here can be illustrated using equation 4 (Fig. 6) by showing the consequences for station-holding performance of varying C_{Lo} (equivalent also to varying W_o) and μ for a range of C_{Do} values.

Rays and plaice have high-lift/low-drag shapes. Modifying lift is seen to be the most effective way of maximizing station-holding speed for such fish (Fig. 6A). In contrast, high-drag and low-lift shapes, such as lasher, obtain little improvement in performance through lift-reducing behaviour. However, station-holding speeds can be improved by increasing μ (Fig. 6B). Hence, the major defence against currents of high-drag/low-lift forms is to increase μ, but this is only possible if there is some surface structure. Note too, that increased μ can make small improvements in station-holding speed for high-lift forms if drag is also high. However, this situation seems unlikely to be seen among animals.

Rays and plaice are not as speciose as more fusiform fish (Nelson, 1976). Although most benthic fish are depressed to some degree, most will have a large fineness ratio, like lasher, and are likely to have relatively low lift and high drag.

Not surprisingly, therefore, mechanisms to increase μ are common among benthic fish. Fish in torrential streams increase μ using suckers to hold station (Hora, 1930). Similarly, stream insects use appendages as grapples, gripping and hooking on epiphytes and in cracks (Hynes, 1970). These fauna also increase μ using adhesives. Intertidal fauna also typically increase μ using suction and adhesives (Denny, 1988). Therefore, increasing μ appears to be the most ubiquitous response to unavoidable flows. ·

The ubiquity of μ-enhancing structures correlates with a wide distribution of animals with low-lift/high-drag shapes in current-swept habitats. In these habitats, surface structure is common, since most currents are unidirectional, removing smaller particles and leaving larger items. The body shape of the more fusiform fish is probably better able to take advantages of cracks between remaining pebbles, boulders, etc. However, the plaice-like form will be successful on tide-swept soft bottoms, especially where flow rates are sufficient to uncover buried animals. Then there is little opportunity to enhance μ, and ability to hold station will depend on body form and behaviour such as fin-beating and body posture. Therefore, it is probably no accident that pleuronectiform and batoid fish are common in these habitats, while the more fusiform benthic fish are more common in structured current-swept situations.

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