THE REACTIONS OF THE PLAICE (*PLEURONECTES PLATESSA* L.) TO WATER CURRENTS

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INTRODUCTION

Rheotropism in fish has been shown to be a response to visual or tactile stimuli resulting from displacement in a water current past an external reference point (Lyon, 1904, 1909; Dykgraaf, 1933). Flatfish resting on the sea-bed could detect the current directly by the flow over the whole body or over the lateral line, which is known to be sensitive to currents (Dykgraaf, 1933; Sand, 1937). Very little is known either of the reactions of flatfish to currents or of their sensory mechanism of current detection. Observations have therefore been made on the reactions of plaice, *Pleuronectes platessa* L., to currents.

MATERIAL AND METHODS

(1) *Apparatus.* Experiments were conducted in a Perspex flume (30 × 32·5 × 550 cm.) which gave fine control of water velocity and depth. A detailed description of this apparatus is given in a previous paper (Arnold, 1969).

(2) *Experimental conditions.* Observations were made on fish up to 28 cm. in length, the majority of which were obtained by longshore beam-trawling at Lowestoft, although a few larger ones (II-group fish in their third year) were caught in a Granton trawl in the vicinity of Smith's Knoll (52°43'N, 02°18' E). Fish were kept prior to use in 450-litre asbestos-cement tanks (base area 96 × 69 cm.) filled with sea water, aerated and held at 10° C. Sea water was obtained from settling tanks 3–4 days after being pumped ashore at high tide from the groyne below the laboratory. The salinity of this inshore water varied between 32·5 and 33·7‰. Fish were fed regularly on *Arenicola* or *Enchytraeus*.

(3) *Experimental procedure.* The flume room was maintained at 10°C, but the re-circulating pump raised the water temperature so that the experimental fish were subject to temperatures between 10 and 15°C. Preliminary observations in a small flume indicated no obvious change in behaviour at temperatures from 20°C down to 2·5°C. Light intensity in the flume, measured with an Eel Lightmaster photometer, ranged from 20 to 400 m. candles under the room lighting (9 × 80 W Crompton 'Daylight' fluorescent tubes.)

Each fish was placed individually in the flume, in still water 10 cm. deep, heading towards the weir, and allowed approximately 5 min. in which to settle down and assume a normal resting posture. Fish were placed in the central section of the flume so that even the largest were completely in the boundary layer, as they would be on the sea bed. A slow current was started by opening the control valve a fraction of a turn

and was increased in small steps until the fish turned to head into the current. If the fish was still, 2–3 min. were allowed at each valve setting, longer if it was active. Subsequently, the velocity was increased by larger steps (approximately 5 cm./sec.) until the fish was displaced. All movements made by the fish were recorded together with the current speed which was measured at the point in the flume where the fish was lying. To allow for the increase in height of the ocular surface from the bottom (that is, the width of the fish) with length, and the decrease in velocity across the boundary layer on the bottom of the flume, the velocity of the current was measured at the level of the top of the operculum. This is the highest constant point of the fish, because although the eyes frequently project further they are highly contractile. The height of the operculum was measured by using the optical instrument on its moving table as a cathetometer. The field of view of the telescope was then confined to this level by clamping a slotted plate to the side of the flume; 3 mm. wide slots were used for measurements in the boundary layer. At low velocities (less than about 5 cm./sec.) a velocity gradient across the slot was seen through the telescope. The measurement was then made at the centre of the slot by fixing the eye on the horizontal scale of the graticule. Particles at this level appeared stationary while those above and below travelled across the field of view in opposite directions. At higher velocities this gradient was not perceptible, but the sinuous paths of the particles made determination of the null point more difficult than in the main stream, where they were primarily rectilinear, and inevitably reduced the accuracy of the measurements. The scale of the optical instrument was read to the nearest half-division which equalled $5 \mu A$. The heights of the centres of the slots above the bottom of the flume varied with the length of the fish as follows:

Fish length (cm.)	Height of slot (cm.)
5–9	0·5
10–14	1·0
15–24	1·5
25–30	2·0

The description of the behaviour given below is based on observations of 60 fish made at various times during 1966 and 1967; 35 more were used in November and December 1968 to complete the data on the relation between behaviour and current speed. All observations were made during the daytime, and the fish were subject to the natural 24-hr. light cycle prior to the experiments. Most observations of behaviour were made with fish on a hard Perspex bottom although a few are described of small fish on a sand-bed.

BEHAVIOUR

(1) *Descriptive terms*

Viewed from above, the plaice is rhomboidal in shape and the outside margins of the dorsal and anal fins form shallow triangles with the longitudinal axis of the body as a base line (Fig. 1). The fin rays project out from the body approximately normal to its edge, except for the extension of the dorsal fin under the head where they project vertically down. In front of the apex of each triangle the distal ends of the rays project beyond the web of the fin and are hooked backwards; behind it the remaining 30 rays or so have no hooks and barely project at all. The upper surface of a resting flatfish may be anatomically either its right or left side according to species. To avoid confusion,

therefore, the upper and lower surfaces are described as ocular and eyeless respectively (Traquair, 1865); in the plaice the ocular surface is the right side. The opercula and the paired fins are described in the same way.

First-year plaice (1·8–9 cm. long) are described as O-group fish, second-year (8–18 cm.) as I-group, third-year (> 18 cm.) as II-group and so on.
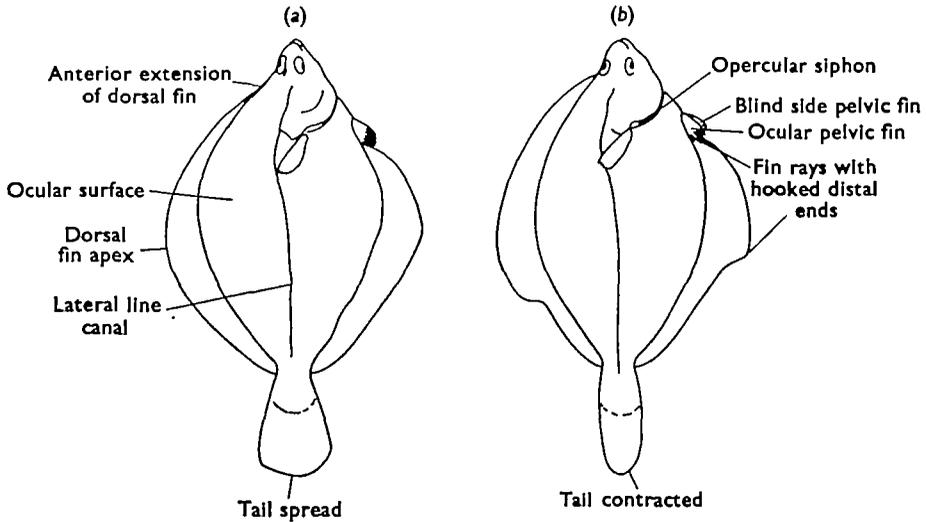

Fig. 1. Outline drawings of plaice to show difference between (*a*) *resting posture* and (*b*) *clamped-down posture.*

(2) *Behaviour in still water*

Most plaice were observed to lie at rest on a hard transparent substrate with the eyeless surface touching the bottom and the pectoral fin folded flat. The tail was usually spread with the bifurcated distal ends of the rays visible. The ocular pectoral fin was folded down on the body with the rays closed, and the ocular pelvic fin was similarly furled; the pelvic fin of the eyeless side was expanded or retracted. Respiratory movements were very slight with usually only the opercular valve on the ocular side showing any rhythmic movement.

The burying movements appeared to be very similar to those of the sole (*Solea vulgaris*), in which several vigorous beats of the head against the sand are accompanied by a lateral wave of muscular contraction travelling back down the body and vertical movements of the marginal fins which throw sand over the ocular surface (Kruuk, 1963).

(3) *Behaviour in currents on a smooth Perspex bottom*

The behaviour observed could be divided into four stages which succeeded one another with an increase in current velocity.

Stage 1. Generally no response. (Approximately 0–8 cm./sec.). Most fish showed no response as the current was started, remaining in the still water posture. Occasionally, a raised fin margin was lowered and, rarely, there were a few isolated beats of the dorsal and anal fins. There was no noticeable increase in respiration rate, nor was any melanophore reaction or eye nystagmus observed.

Stage 2. Head upstream orientation. (Approximately 0·8–30 cm./sec.). As the current was increased, most fish turned to head upstream, generally without leaving the bottom and accomplishing the turn by movements of the fins and tail. This initial turn is described as the orientation threshold. Some fish remained heading upstream while the current velocity was increased, but most turned about freely over a range of velocities, even heading downstream again. In this last orientation, the ocular pectoral fin and the extreme tip of the tail were often raised by the current. Because of this change in orientation, stage 2 has been subdivided into two phases: (a) in which the free movement occurred and (b) the subsequent stage at higher velocities when the fish no longer voluntarily changed its heading.
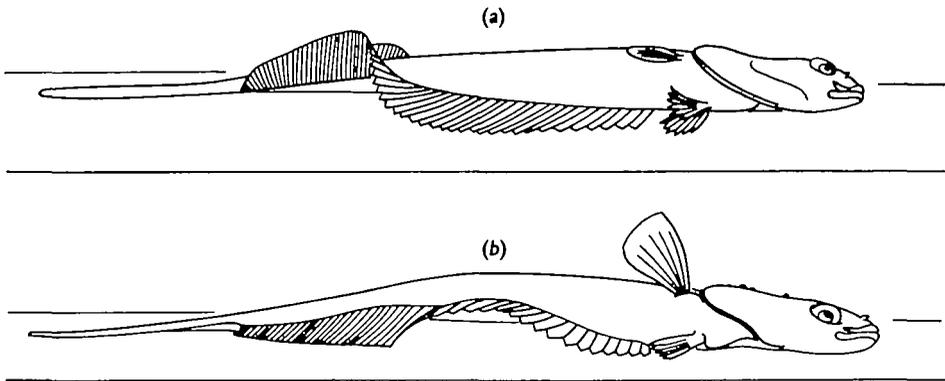

Fig. 2. Sketches (from photographs) of (a) *raised fin posture*, showing region of dorsal and anal fins involved in *posterior fin-beating response* and partially-erect ocular pelvic fin; (b) *arched-back posture* with central areas of marginal fins raised and ocular pectoral fin erect.

(a) (Approximately 0·8–20 cm./sec.). When heading into the current, the tail was usually closed and the margins of the fin rays closely opposed to the bottom. Burying movements often occurred, particularly after a fish had moved or changed its orientation, and after these a *clamped-down posture* was observed. The marginal fin rays were pressed tightly against the bottom and, with the exception of the last two or three, those behind the apex were directed forwards, thus changing the outline of the fish (Fig. 1 b). The *clamped-down posture* did not always occur during this stage and some fish would lie still with parts of the fin margins raised off the bottom (Fig. 2a), giving occasional beats of the posterior parts of the fins. The respiratory movements of the mouth and the ocular operculum increased markedly both in amplitude and frequency.

(b) (Approximately 20–30 cm./sec.). Burying movements and the *clamped-down posture* occurred more frequently with an increase in current velocity. A *posterior fin-beating response*, which had appeared sporadically in the first phase of the stage, occurred more often, becoming nearly continuous at higher velocities. The posterior regions of both dorsal and anal fins were involved; a wave produced by successive movements of the fin rays travelled backwards along each fin from the apex to the tail. If the fish was heading along the axis of the current, the beating of the two fins was symmetrical and synchronized, but if it was heading diagonally across the axis then usually only the downstream fin showed the response (Fig. 3). As the current

was further increased, the fish developed an *arched-back posture* (Fig. 2*b*). At rest, the back of a plaice slopes gradually down from the operculum to the tail and the same profile was seen in fish which had just settled in a fast current. After a few minutes the caudal half of the body gradually rose until the back was almost level for two-thirds of the distance behind the pectoral fin. The inner margins of the dorsal and anal fin were raised so that the fin rays arched steeply up from their tips; some fish raised the margins of the fins at the apex, but this was usually in phase (*a*) when this posture also occurred occasionally. Most fish showed a strong *posterior fin-beating response* when this posture was developed and after several strong beats returned to the *clamped-down posture*. Fin erection was another feature of this stage but varied considerably from one fish to another. One individual kept its ocular pectoral fin erect all the while it was in the current and the fin was turned on its base by the current according to the direction in which the fish headed. The ocular pelvic fin was spread frequently by most fish. It was held parallel to the bottom of the flume or raised nearly vertical with the tips of its rays pointing forwards to give it the shape of a spoon (Fig. 2*a*).

Stage 3. Slipping and swimming. (Approximately 25–40 cm./sec.) With a further increase in current velocity the fish began to be displaced slightly downstream. Occasional slips of as much as 5 cm. were observed to which the fish responded by paddling movements of the marginal fins, moving upstream again and re-settling, usually with burying movements. The fish generally regained most or all of the ground lost. Erection of the ocular paired fins occurred frequently just before slipping and again after settling, but this did not accelerate or check displacement. Between successive slips the behaviour was the same as in stage 2*b*.

As downstream displacement became more frequent, the fish responded with bursts of swimming and, keeping clear of the bottom, often moved 10–20 cm. upstream. Most fish were progressively displaced to the weir at the downstream end of the flume but were still capable of swimming upstream against the current for 1–2 m. If the fish was displaced so that its tail touched the weir a burst of very strong swimming upstream was observed.

Stage 4. Displacement. (Approximately 45–75 cm./sec.). Finally, as the current was increased again the fish was displaced over the weir.

(4) *Behaviour in a current on a sandy bottom*

Observations were made on 15 O-group fish in a small 14 cm. wide flume (in use before the 30 cm. flume was completed) with 10 cm. depth of water and a 2·5 cm. deep bed of Lowestoft beach sand (80–90 % fine sand, range of particle size, 125–250 μ).

As soon as they were put in still water in the flume most of these fish buried themselves in the sand, leaving only the eyes showing. There were no fin movements nor obvious respiratory currents so that their position was only revealed by the twin black pupils of the eyes, which had a characteristic asymmetry. Those fish which remained on the surface of the sand turned to head upstream in the same range of current speeds as on a Perspex bottom and then usually buried themselves. Others, which were already buried, remained in their original orientation until the sand was eroded from around them. Erosion started at a current speed of approximately 24 cm./sec., measured 0·5 cm. above the sand-bed. With buried fish heading upstream, erosion first appeared

as a small scour round the point of the jaw, which slowly advanced along the leading edge of the body to the apex of the fins. The fish then usually swam upstream. When small sand waves began to appear (stream speed approximately 20–25 cm./sec.) and moved slowly downstream, buried fish stayed put, allowing themselves to be completely covered while the wave passed over them. The sand was scoured away in some of the troughs between the waves exposing the bare Perspex bottom.

(5) *Behaviour in the dark*

Observations were made in the dark with an infra-red viewer. The flume room was completely blacked out with double blinds over the windows and curtains over the door. Sources of infra-red radiation (100 W. tungsten bulbs behind Pilkington OX 5
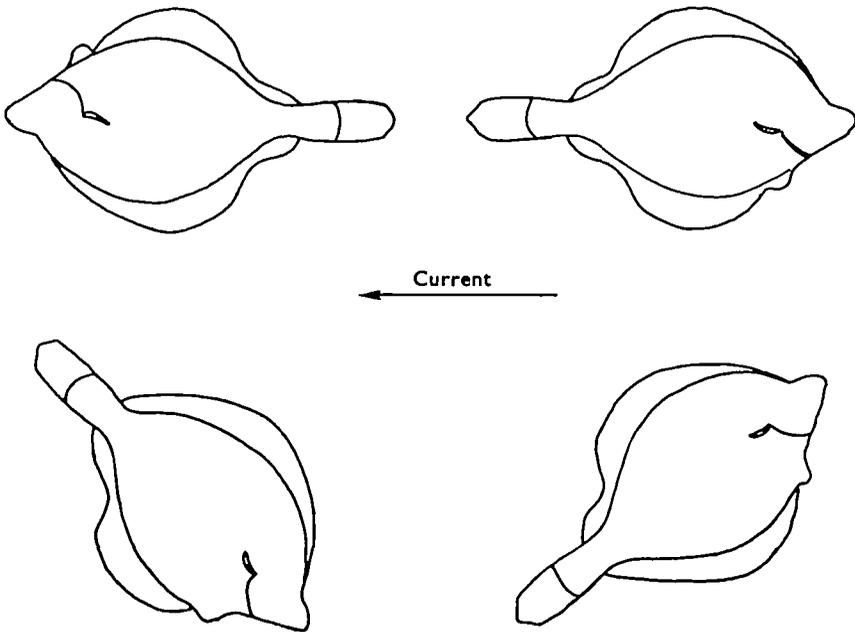

Fig. 3. Outline drawings of plaice to show relation of *posterior fin-beating response* to direction of current

filter glass) were mounted inside the supporting frame below the flume so that fish were observed against an 'illuminated' background. There is no evidence that fish can detect infra-red radiation (Duncan, 1956) and no observations were made that would suggest that plaice do so.

Fish on either a Perspex or a sandy bottom showed the same behaviour in the dark as in the light and orientated to face the current at speeds within the same range (Fig. 3). In the dark most fish swam more often than in the light and when touching the wall of the flume could swim upstream against the current. Fish in midwater were, however, displaced downstream, often swimming gently as they went, and heading in all directions. Some were displaced over the weir, others touched the weir plate or the wall near it and rapidly reorientated. At higher velocities fish on the bottom swam vigorously against the current (stage 3 above), while those in midwater were displaced

over the weir. Fish released in midwater in the dark in a stream velocity of 40–50 cm./
sec. were swept downstream and did not orientate unless they touched the wall, or
more usually, the bottom of the flume.

(6) *Relation of behaviour on smooth Perspex bottom to current velocity*

In order to clarify the description given above and because there was a great deal
of variation in the current velocity at which different fish showed the same response,
each of the four stages of behaviour has been related to a range of velocities. The
measured velocities at which 35 fish turned to head into the stream, began to swim
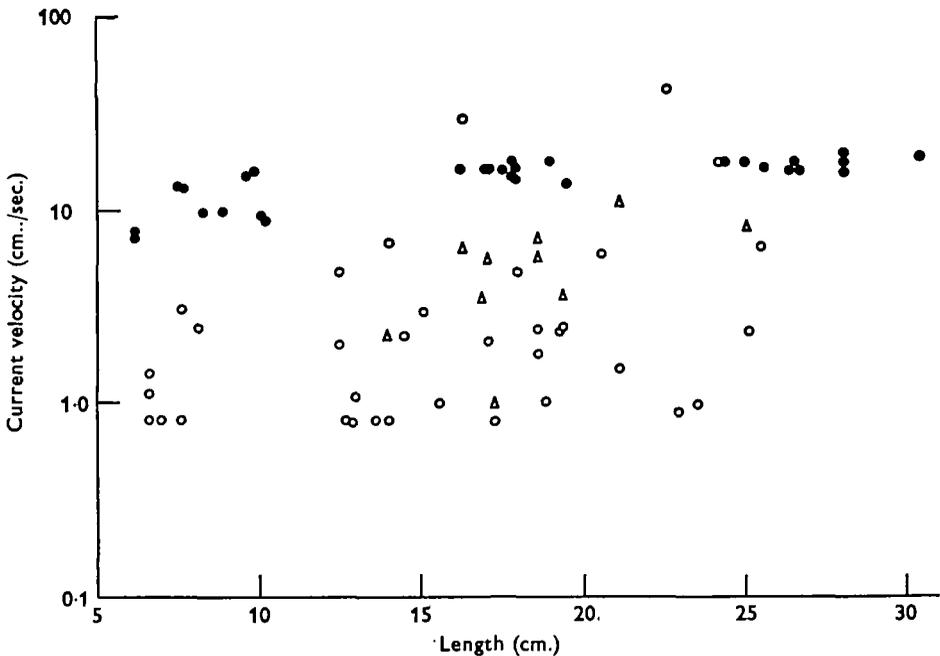against it and were finally displaced over the weir are shown in Figs. 4 and 5.

Fig. 4. Current velocities at which plaice on a smooth Perspex bottom turned to head into the
current and anaesthetized fish heading upstream were displaced. O, Orientation in light; △,
orientation in dark, ●, Displacement of anaesthetized fish facing upstream.

There was no increase in orientation threshold with length, and for 32 of the 35 fish
the velocity at which orientation occurred was in the range 0·8–8 cm./sec. Some plaice
did not orientate until very much higher velocities and then only when they began to
slip along the bottom. Several fish began to turn near the side of the flume but stopped
when they touched the wall and lay heading diagonally downstream with a leading
edge against the side. Sometimes a fish in this position backed away and turned to
head into the current, but more often it swam on downstream against the wall and
subsequently accomplished its turn in the opposite direction. In these circumstances
the wall of the flume had an obvious guiding effect and delayed the initial orientation.

There was considerable variation in the current velocity at which fish began to swim
against the current (Fig. 5), but O-group fish showed a tendency to swim at lower

current velocities than larger fish. The latter usually showed this behaviour only after they had begun to slip downstream along the bottom despite a vigorous *posterior fin-beating response*. The current velocities at which fish were finally displaced downstream and over the weir are also shown in Fig. 5. These are mainstream velocities for fish which swam in midwater, but for those which swam along the bottom they were measured at the appropriate height. Again, there was considerable variation in the
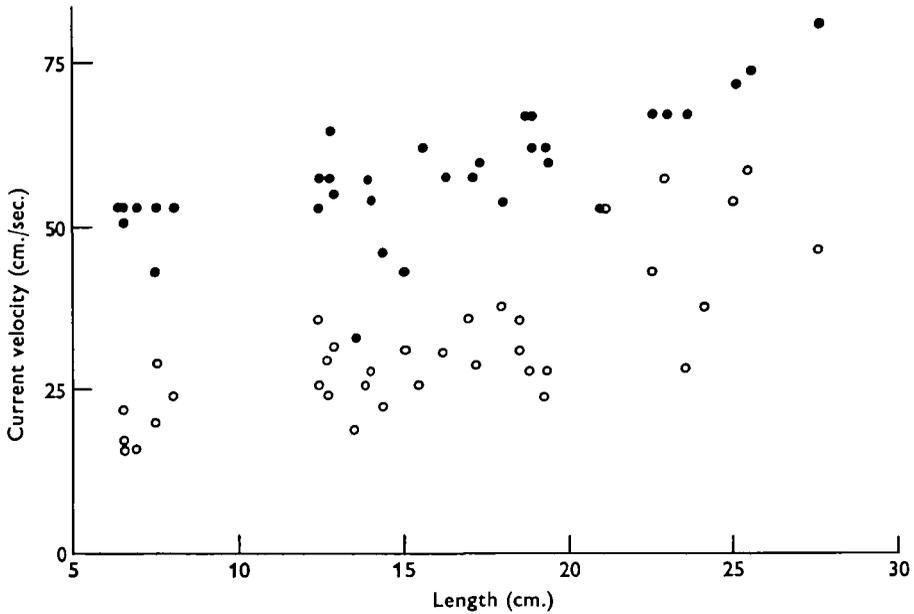

Fig. 5. Current velocities at which plaice began to swim upstream and at which they were displaced from the flume. O, Beginning of swimming phase; ●, displaced over weir.

Table 1. *Ventilation rates of individual fish in still water and in a current of 30 cm./sec.*

	Current speed (cm./sec.)						
	0		30				
Fish length (cm.)	Mean ventilation rate (beats/min.)	s.D.	Mean ventilation rate (beats/min.)	s.D.	Increase in mean ventilation rate (beats/min.)	t	P
23·2	28·5	1·2	34·2	2·9	5·8	5·9	0·001
25·0	34·3	0·8	45·5	1·8	11·2	17·8	0·001
26·6	29·0	2·6	32·9	0·9	3·9	4·4	0·01
27·4	28·4	1·6	38·9	6·7	10·5	4·9	0·001
29·2	28·2	2·0	38·0	3·8	9·8	7·2	0·001

vigour with which individual fish swam against the current and hence the displacement velocity. There seemed, however, to be a general increase from approximately 50 cm./sec. with 6·5 cm. fish to 70 cm./sec. with 25 cm. fish.

The change in respiratory movements observed in fish subject to a current after being in still water has been mentioned (p. 684). With increased movements, a greater volume of water was taken in and expelled per cycle and the rate of ventilation also

increased. The time taken for ten respiratory cycles was measured for five fish in still water and in a current of 30 cm./sec. There was a significant increase in mean ventilation rate (Table 1).

HYDRODYNAMIC FACTORS

The overall picture of the behaviour suggests that the plaice reacts to the current to avoid being swept away. It is therefore of interest to consider its behaviour in relation to hydrodynamic factors.
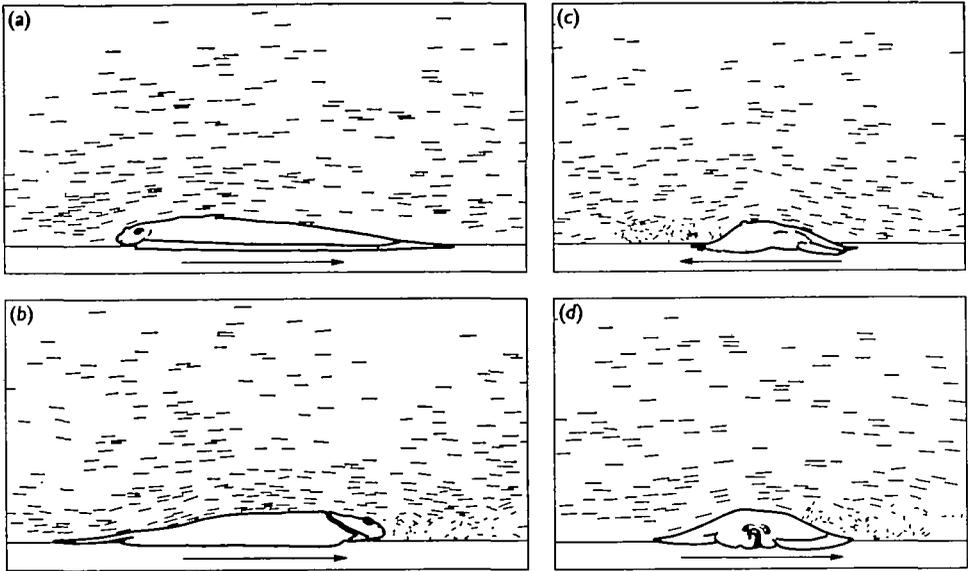

Fig. 6. Streamlines over a 22 cm. plaice in a current of 30 cm./sec. (at level of top of operculum) visualized by photographing cellulose acetate particles in a vertical beam of light (from photographs).

(1) *Streamlining.* The metamorphosed plaice is streamlined and its sagittal profile is very similar to that of an aerofoil. The effectiveness of the streamlining was observed by photographing flow patterns round a live fish resting on the bottom of the flume. A suspension of cellulose acetate particles was photographed as it passed through a vertical light beam (Ambühl, 1959) positioned over a fish. The flume room was in darkness and an exposure of 1/30 sec. was used with an aperture of f 1·9 (Ilford HP 3 film). Fig. 6 shows that only when the fish faced upstream was it completely streamlined; otherwise turbulence developed on the lee side.

(2) *Anaesthetized fish.* Fish anaesthetized in MS 222 (Sandoz) were used as 'models' to study the physical behaviour of the body form. When heading downstream, the tail was lifted by the current, first at the tip and then along the whole length, followed by the peduncle and the posterior part of the body until the fish was displaced just off the bottom. The head was lifted in the same manner when the fish was facing upstream and in this case the fish 'took off', climbing steeply up to the surface and at the same time being displaced. Gradually the angle of the body to the axis of the stream

increased until, when virtually standing on its tail, it stalled and fell back to the bottom, usually slipping sideways. Occasionally the head was turned downstream past the tail, with the fish resting on a cushion of water a few millimetres thick. The current veloci- ties at which anaesthetized fish heading upstream were displaced are shown in Fig. 4. Fish heading downstream appeared to be displaced at lower velocities and for fish 24–30 cm. long the difference was shown to be significant (Table 2).

Table 2. *Current speeds at displacement of anaesthetized fish (24–30 cm.) facing upstream and downstream*

	Current speed (cm./sec.)	
Length (cm.)	Head upstream	Head downstream
26·4	17·8	11·5
28·0	17·7	10·9
30·3	18·8	10·9
26·3	16·5	11·5
28·0	16·5	13·2
26·5	16·5	13·2
24·8	17·8	13·4
24·2	17·7	16·1
28·0	20·0	13·2
25·5	17·1	13·9
Mean	17·6	12·8
Standard deviation	1·1	1·6

$t = 7.8$; D.F. $= 18$; $P < 0.001$.

(3) *Undercurrents.* In a resting plaice the marginal fins make close contact with the bottom and on its dorsal side the fish has a complete fin curtain from tail to head, completed by the anterior extension of the fin (Cole & Johnstone, 1901). However, on the ventral side there is a gap extending from the jaw to the pelvic fins and leading under the body. When the fish is buried this gap will be filled with sand, but if the fish is not buried water can penetrate beneath it at this point. This was demonstrated by introducing a solution of potassium permanganate under the fish, the flow patterns being observed in mirrors suspended below the flume. A number 18 hypodermic needle was bent into an obtuse angle, so that its tip could be inserted just under the margins of the fins. The solution was injected gently to avoid disturbing the existing flow patterns. The patterns observed are shown in Fig. 7. Lying across the current with the anal fin upstream, the fish presented the largest gap in the protective fin curtain to the current. Dye injected here either flowed around the pectoral fin and out between the snout and dorsal fin or back along the inner margin of the anal fin. It was then either ejected by beating of the posterior part of the dorsal fin or, when this was clamped down, turned forward joining the broad stream from the peduncle along the inner margin of the dorsal fin to the head (Fig. 7a). If the dorsal fin was lifted the current flowed directly across and the rate of flow was increased (Fig. 7b). With the dorsal fin upstream, the pattern was reversed (Fig. 7c). In both positions, small flows occurred between the rays of the upstream fin. With the fish heading upstream very little water penetrated beneath it as long as the marginal fins were pressed close to

the bottom; small flows moved slowly back and formed a swirl (Fig. 7*d*). When the *posterior fin-beating response* occurred, the water was ejected downstream in bursts. If the fins were held open, and especially if the back was arched, a steady flow of water was observed under the fish (Fig. 7*e*). If the fish headed downstream, this flow pattern was reversed; the beating of the posterior parts of the marginal fins then ejected water
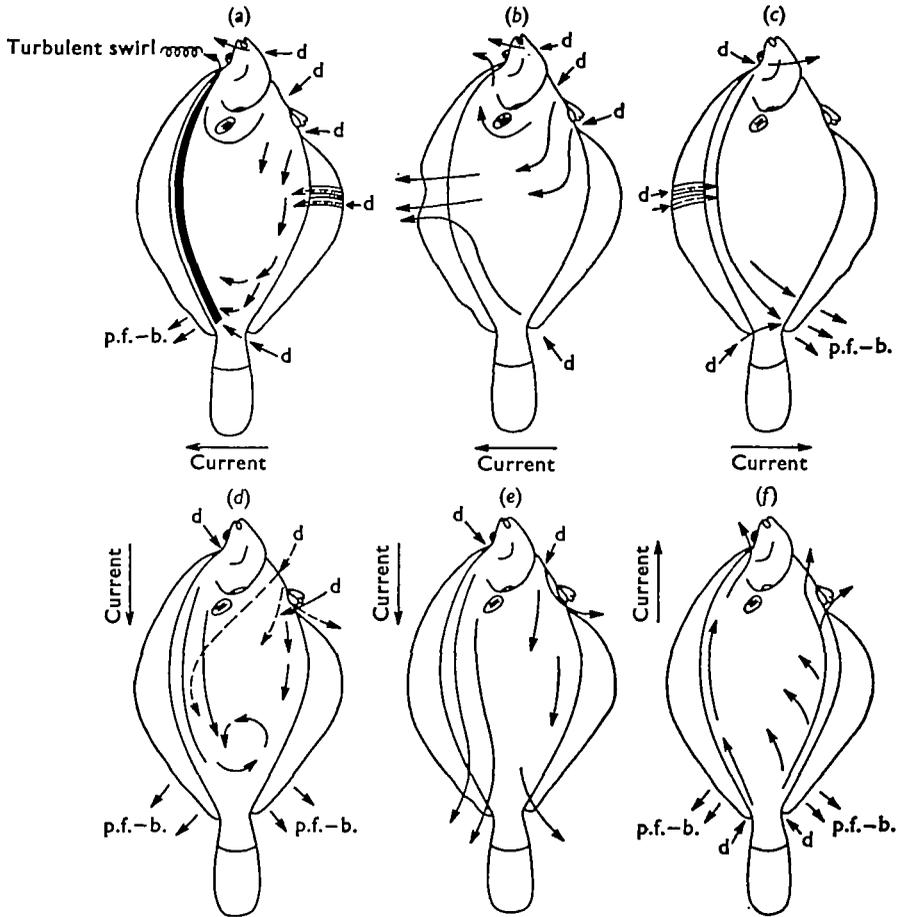

Fig. 7. Currents beneath a 22 cm. plaice on a smooth Perspex bottom, demonstrated by injecting potassium permanganate solution. Point of injection—d, *posterior fin-beating response* —p.f.-b.

against the current (Fig. 7*f*). These observations demonstrated clearly that the function of the *posterior fin-beating response* was the removal of water from beneath the fish.

(4) *Asymmetric gill action.* Respiratory currents were also observed by injecting permanganate solution into the mouth. With a fish at rest in still water, dye was expelled entirely through the siphon of the ocular operculum. Only if the fish moved was dye also ejected from the underside operculum. Only the ocular side operculum was used by fish resting in a current on the bottom. This was so even when the venti-

lation movements were very large and the whole of the opercular opening, and not just the siphon, was in use.

(5) *Development of arched-back posture.* There was individual variation in the development of this posture and no simple relation was found between current velocity and the distance between the under-surface of the fish and the bottom. This distance was measured acoustically with a Mk 2*b* Ultrasonoscope using an immersion probe (type 23/W/2½) held vertically above the fish at a frequency of 5 MHz. The most accentuated postures appeared at relatively low velocities in stage 2(*a*) of the behaviour, but at higher velocities the continuous pumping action of the *posterior fin-beating response* prevented the ocular surface rising so high. Fish of about 25 cm. length maintained the under-surface approximately 0·5 cm. off the bottom by continuous beating of the fins. Even at maximum arching, the tips of the marginal fin rays could still touch the bottom, although portions of the fins were sometimes raised. One fish 29 cm. long showed a maximum height above the bottom of 1·6 cm. at a current speed of 17 cm./sec. The most important feature of this posture was its gradual development, which appeared to be quite passive in contrast to its rapid and active removal by the *posterior fin-beating response.*

SENSORY MECHANISM

The rheotropic behaviour of plaice in midwater disappeared in the dark, indicating that this was an optomotor response, as Lyon (1904) originally showed for *Fundulus.* On the bottom in the dark, however, orientation still occurred, showing that a tactile stimulus alone could elicit this response. This was in agreement with Dykgraaf's (1933) findings for blinded minnows, but the tactile stimulus to which his fish responded arose from their displacement when in contact with the bottom or sides of the tank. Plaice, however, headed into the current at a velocity well below that at which anaesthetized 'model' fish were displaced, suggesting that slipping of the fish along the bottom was not an essential stimulus for orientation. Experiments were therefore made with water jets to see if fish on the bottom would respond to the direct stimulus of the water flow.

A continuous fine jet of sea water was used to test the responses of 10 fish (10–20 cm. length) in a small Perspex tank (60 × 30 × 12 cm. depth of water). A false floor perforated with small holes (0·6 cm. diameter at 1·3 cm. centres) was used to study the reaction to jets from the eyeless surface. All fish responded in the same way and the only variable factor was the force of the jet required to elicit the response; this increased with the size of the fish but no attempt was made to measure it.

Three areas were found on the ocular surface where stimulation produced a behavioural response. These were the two leading edges of the body on each side of the head, as far back as the dorsal and anal fins (Fig. 8) and the tail. The sensitive region on each side of the head was confined to a small area above and below the leading edge itself, and stimulation produced a slow *posterior fin-beating response.* This also occurred if the right nasal papilla (Fig. 8) was stimulated, and in some fish was then accompanied by erection of the ocular pelvic fin. A strong jet on the papilla elicited the fully erect spoon-shaped posture of this fin described above. The most striking response was obtained when a jet of water was played on the tail. Stimulation

of its top or tip resulted in its rapid closure and a strong fin-beating response; it was particularly sensitive to a jet directed horizontally from behind. No response was obtained from stimulation of other parts of the ocular surface; jets were directed at the lateral line, the eyes, fin rays and into the opercular siphon without effect. The under-surface of the tail was also found to be very sensitive but stimulation of the rest of the
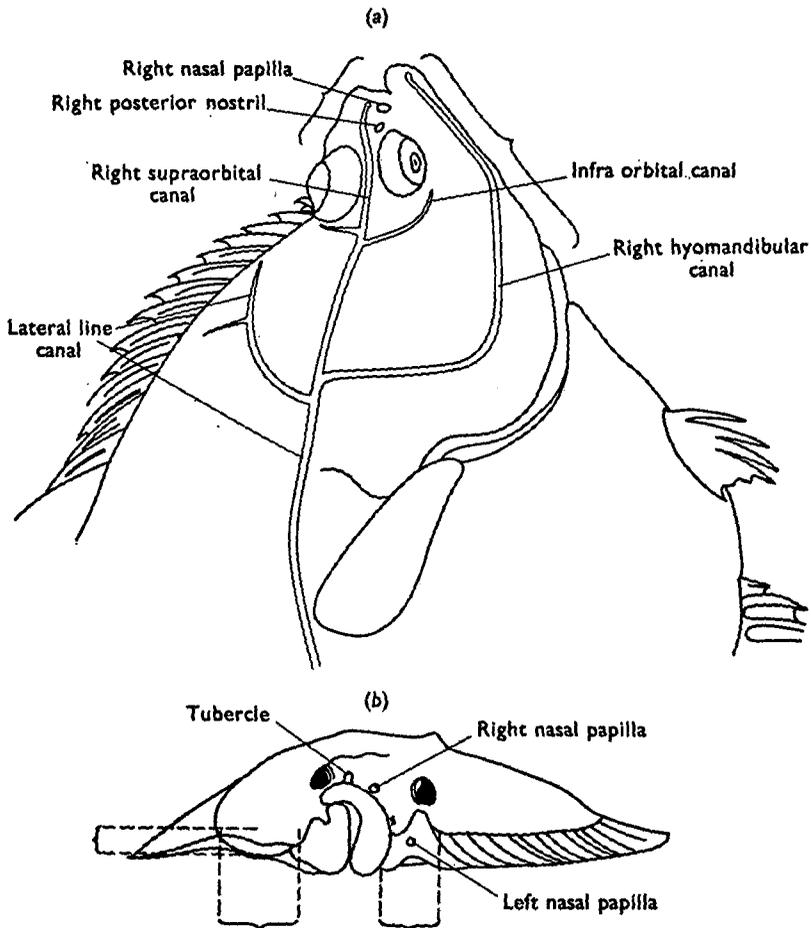

Fig. 8. Head of plaice to show hyomandibular and supra-orbital canals, nasal papillae and the areas whose stimulation by water jets elicited a behavioural response. These areas are indicated by brackets. (a) Ocular surface, (b) anterior view. Position of sensory canals taken from Fig. 23 of Cole & Johnstone (1901).

surface generally produced no response. Occasionally, after persistent stimulation a slight beating of the marginal fins occurred when the jet was directed at them.

Since stimulation of these areas by water jets elicited the same behavioural responses that were shown in a current, it can be concluded that they are the main areas which respond to the tactile stimulus of the current. A shearing stimulus between the fish and the bottom may therefore not be involved in the detection of the current.

DISCUSSION

Despite an extensive literature on rheotropism little is known about the thresholds for the response. Velocities at which plaice orientated to the current ranged mainly from o·8 to 8 cm./sec. and these values agree quite well with Dykgraaf's (1933) observation that a velocity of 4–5 cm./sec. was required to produce an orientated response of blind minnows (*Phoxinus phoxinus*) in contact with the bottom. They are higher, though, than those of o·4–o·5 cm./sec. arrived at statistically by Gregory & Fields (1962) for juvenile silver and Chinook salmon (*Oncorhynchus kisutch* and *O. tshawytscha*), which were blinded or observed in the dark. Three authors have given measurements of thresholds for optomotor responses. Harden Jones (1963) found that several marine fish (*Clupea harengus* L., *Osmerus eperlanus*, L., *Gadus morhua* L., and *G. luscus* L.) responded to a striped background moving at 1–2 cm./sec. These results agree well with those of Houston (1959), who found that a speed of 2–3 cm./sec. evoked a mild response in chum salmon fry (*O. keta*), and Brawn (1960), who found that herring (*C. harengus*) held captive in a cage suspended in a tidal current responded to currents of 3–9 cm./sec. The lowest published threshold is o·02 cm./sec. for an optomotor response by a pike (Harden Jones, 1958).

The behaviour of plaice in heading into the current appears to be adaptive in several ways. First, it has been shown that in this orientation it is streamlined; it will therefore offer minimum resistance to the current and need minimum effort to maintain position. This is confirmed by the observation that anaesthetized fish heading upstream are displaced at a significantly higher velocity than those heading downstream. Secondly, if the fish heads downstream, the tail is very vulnerable and easily lifted by the current. Thirdly, the *posterior fin-beating response* is most efficient in removing water from the under-surface when the fish heads upstream, because both fins are used and the ejected water is carried away by the current. The efficiency of this response in ejecting water astern is high since the resultant force is parallel to the direction of expulsion; the posterior parts of the marginal fins have the same position as the median fins of the balistid fish *Monocanthus hispidus* (Harris, 1937). Fourthly, if the fish is displaced it can more readily recover its station by free-swimming when it heads upstream. Finally, the asymmetric opercular action avoids exhaling a respiratory current beneath the fish, which would tend to lift it off the bottom. Schmidt (1915; in Norman, 1934) has pointed out the disadvantages of this in still water; it would be even greater in a current. Yazdani & Alexander (1967) have described the existence of a channel connecting the two opercular cavities in flatfish which allows water to flow equally over both sets of gills and be expelled through the ocular operculum only. It would appear to be hydrodynamically advantageous for the fish to head into the current, but one possible disadvantage of this may be the development of the *arched-back posture*. This appeared to be produced not by the fish itself but by the lift effect of the water flowing over its streamlined shape. Water then gradually flowed in under the fish to fill the resulting space, collecting there for as long as the marginal fin curtain was held against the bottom.

Sensitivity of the skin all over the body to the stimulus of the current is likely and could only be excluded if the tactile sense were removed entirely. It is evident, though, that the sense organs used by the plaice in detecting currents are grouped primarily in

the three areas described, and the distribution of these is striking. They are all places where there is no protective fin curtain and where water is most likely to penetrate beneath the fish. When the fish is buried in sand the area around the right nasal papilla may be exposed as well as the eyes, so that it is likely to be important in current detection. Dykgraaf (1933) showed that the lateral line played no part in the tactile orientation of blind minnows (*Phoxinus phoxinus*) to a current, although it was the informative sense organ in midwater orientation to jets of water. It is evident that although the lateral line of the plaice can detect water jets, it similarly plays no part in the rheotactic behaviour. It must be pointed out, though, that two canals are present in the sensitive areas of the head (Fig. 8). The hyomandibular canal runs along the right-hand leading edge of the body on both ocular and eyeless surfaces, and the right supra-orbital canal and vestiges of the left lie in the region of the right nasal papilla (Cole & Johnstone, 1901).

With no observations of its behaviour in the sea and very little information on the speeds of bottom currents, it is impossible to evaluate fully the importance in the ecology of the metamorphosed plaice of its response to currents. Few observations of near-bottom current speeds have been made on or near grounds where plaice occur. Carruthers (1962), using a jelly bottle technique, recorded speeds from 20 to 120 cm./ sec. at 15 cm. off the bottom on Caister Shoal, off Great Yarmouth; Jones, Kain & Stride (1965) similarly measured a speed of 51 cm./sec. at 30 cm. off the bottom on Warts Bank, Isle of Man. McCave (personal communication) has calculated current speeds of up to 40–50 cm./sec. at 10 cm. above the sea-bed in the region of the West Hinder Bank in the southern North Sea. He measured speeds at four levels between 30 and 160 cm. above the bed and extrapolated on a logarithmic curve fitted to the results. There are still, however, no direct measurements in the vital few centimetres immediately above the bottom. In addition to tidal currents, the sea-bed of the continental shelf is subject to considerable wave action, and Stride (1963) gives a calculated value of 103 cm./sec. for the strongest oscillatory current. This figure referred to a force 10 gale in 90 m. depth of water in the English Channel. It is clear even from this scanty information that the combined effect of tidal and oscillatory currents must be an important environmental factor in the life of the plaice on the sea-bed.

It has been argued (Verwey, 1958) that the plaice uses tidal currents to obtain directional clues on migration, and the present observations show that plaice can detect the direction of a current as slow as 1 cm./sec. However, the observed rheotropic behaviour may be significant as a compensatory reaction to a physical factor of the environment and may not be involved in migration. Lyon's (1904, p. 160) conclusion that rheotropism in fishes is a form of compensatory motion which explains orientation, but not migration, should be stressed in this connexion.

SUMMARY

1. Observations were made on the reactions of plaice (2–28 cm. length) to water currents in a small flume (30 × 32·5 × 550 cm.), and a behaviour pattern is described.

2. At a threshold velocity fish turned to face upstream, usually showing burying movements or a *clamped-down posture*. With increasing current velocity they remained on the bottom, showing a *posterior fin-beating response*. Fish displaced by the current

reacted firstly by moving upstream on the bottom and re-settling and at higher veloci-
ties by bursts of swimming in midwater. A velocity was finally reached at which each
fish was displaced downstream over the weir.

3. On a sandy bottom small buried plaice did not usually react to the current until
the covering layer of sand was eroded away.

4. Observations with an infra-red viewer showed that although the typical opto-
motor response shown in midwater disappeared in the dark, behaviour on the bottom
remained the same as in the light.

5. The lowest velocity at which fish turned to face the current was 0·8 cm./sec. and
most fish orientated at a velocity below 8 cm./sec.; there was no increase in threshold
velocity with length. There was great variation in the velocity at which individual fish
were finally displaced, but there was a general increase with length from 50 to 70
cm./sec.

6. A displacement velocity was found for anaesthetized fish (24–30 cm. length)
heading upstream, which was significantly higher than for those heading downstream.

7. Photographs of the flow patterns over live fish on the bottom showed that they
were most effectively streamlined when heading directly upstream. Injection of dye
showed that water penetrating beneath the fish was ejected by the *posterior fin-beating
response*, and that the operculum of the ocular surface only was used to exhale water
from the gills.

8. Experiments with water jets demonstrated three areas whose stimulation
elicited a behavioural response shown in the current. These were the leading edges
of the body on either side of the head, including the right nasal papilla, and the tail.

9. The results are discussed in relation to the ecology of the plaice and the contra-
natant theory of fish migrations. It is concluded that the observed behaviour is
hydrodynamically advantageous in maintaining station on the sea-bed.

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