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The movements of plaice *(Pleuronectes platessa L.)* tracked in the open sea

M. Greer Walker, F. R. Harden Jones and G. P. Arnold

Fisheries Laboratory, Lowestoft, Suffolk NR33 OHT, England

Plaice fitted with 300 kHz acoustic transponding tags were tracked by sector scanning sonar off the East Anglian coast for periods up to 54 h and over distances up to 61 km. Using horizontal (plan) and vertical (elevation) scanning, the tracking technique enabled a fish to be positioned to within $\pm 2{\cdot}5$ m in range and 1° in bearing from the research ship, and to within ± 1 m in depth. The position of the research vessel was determined by reference to the Decca Navigator system with a maximum variable error of ± 45 m by day and ± 90 m by night. After release a fish was kept under continual surveillance and a complete record of its movements in the sea was reconstructed from the sonar data recorded during the track. Water current measurements were made during some tracks. Plaice which moved more than 15 km usually came off the bottom at slack water, moved downstream with the tide in midwater and returned to the bottom at the next slack water. When on the bottom the fish showed little or no movement during the opposing tide. The semi-diurnal (12 h period) vertical movements were clearly related to the tidal cycle, ascents being more closely linked to slack water than descents. The regular pattern of behaviour – here called *selective tidal stream transport* – could provide a quick and economical means of movement for fish on migration through areas with strong tides. The observations are discussed in relation to the results obtained when midwater trawling for plaice along the line of their migration route in the Southern Bight of the North Sea. Other aspects of plaice behaviour observed during the tracking are discussed in relation to ship's noise, weather, bottom topography, the energy cost of migration, sensory clues initiating and controlling migration, orientation in midwater, and the development of telemetering acoustic tags.

Introduction

Water currents could provide both a transport system and directional clues for migrating fish which drift passively with the current or orientate to the flow and swim with or against the stream. If migration depended only on *passive* drift, the movements of the population would be determined by the residual current. Some measure of independence from the residual could be obtained through *modulated* drift, the fish joining and leaving the stream in response to the current itself, or some other stimulus, such as light (Harden Jones, 1968; Arnold, 1974).

Vertical migration provides a simple basis for modulated drift, and Hardy (1936; 1953) drew attention to the implications that this could have for plankton. Many marine fish move from the bottom by day into midwater by night (Woodhead, 1966; Blaxter, 1975) and Harden Jones (1965) suggested that migration could involve a combination of passive drift at night and orientated movement during the day. But some fish have been shown to leave the bottom on a particular tide independently of a daily pattern of vertical migration. Each spring large numbers of elvers (*Anguilla anguilla*) enter the Dutch Waddensea through the Marsdiep tidal inlet on their way to freshwater. During the flood stream the elvers are off the bottom and appear to be transported passively inshore, but they are on the bottom during the ebb and are not displaced seawards again (Creutzberg, 1961). In the North Sea, pre-spawning soles (*Solea solea*) are sometimes observed drifting passively at the surface when the tide is flowing towards their coastal spawning area. De Veen (1967) who analysed reports collected from Dutch fishermen, suggested that these soles leave the bottom at night and join the appropriate tide for passive transport during their spawning migration. The results described in this paper confirm and extend de Veen's hypothesis, and show that plaice can move considerable distances in the open sea by *selective tidal stream transport*. The essential behavioural mechanism would appear to be a semi-diurnal[1] vertical

[1] Meaning a vertical migration with a period of about 12 h. As there are close relationships between the behaviour of the fish and periodicity of the tides, the terms diurnal, semi-diurnal, and quarter-diurnal are here used in the same context as in physical oceanography (see Defant, 1958, p. 48) to describe cycles with periods of about 24 h, 12 h, and 6 h respectively.

migration, the fish leaving the bottom at slack water to join one tide rather than another, and returning to the bottom at the next slack water.

Methods

Transponding acoustic tags were fitted to plaice (*Pleuronectes platessa*) which were released singly and followed from RV "Clione" using the Admiralty Research Laboratory's 300 kHz sector scanning sonar. The position of the research ship was determined by reference to the Decca Navigator system. During the period 20 February 1971 to 21 April 1972, 12 plaice were released and tracked off the East Anglian coast, the time of surveillance ranging from 25 to 55 h and the point to point distance covered by the fish ranging from 9 to 61 km. During some of these tracks measurements were made of the velocity of the water currents at the depth at which the fish were swimming.

The fish

The plaice were caught by otter trawl in the southern North Sea in the Silver Pits (54°5′N 2°20′E) and on the Borkum Ground (53°55′N 6°10′E). Fish in good condition and over 35 cm long were taken back to the laboratory and held for about 2 months in tanks of 227 l capacity with 2–3 fish per tank. The bottom of each tank consisted of a biological gravel-bed filter operated by an airlift (Spotte, 1970), which filtered the water in the tank once an hour. In addition a continual trickle of sea water running to waste changed the water in each tank once every five days. The salinity was 32–34 S ‰ and the temperature ranged from 8–14°C. The tanks received natural illumination but were not exposed to direct sunlight. The fish were fed twice a week to satiation with fresh lugworm (*Arenicola marinus*).

Two weeks before a tracking exercise fish which were free from injuries or abrasions, and of normal colouration and lively behaviour, were weighed, measured, sexed and tagged with Petersen tags. Immediately before sailing several fish were taken on board RV "Clione" and held on deck in large aged galvanised iron tanks (capacity about 1000 l) containing clean sand to a depth of 10–15 cm. Once clear of port a continuous flow of sea water (30 l min^{-1}) was maintained through the tanks which were

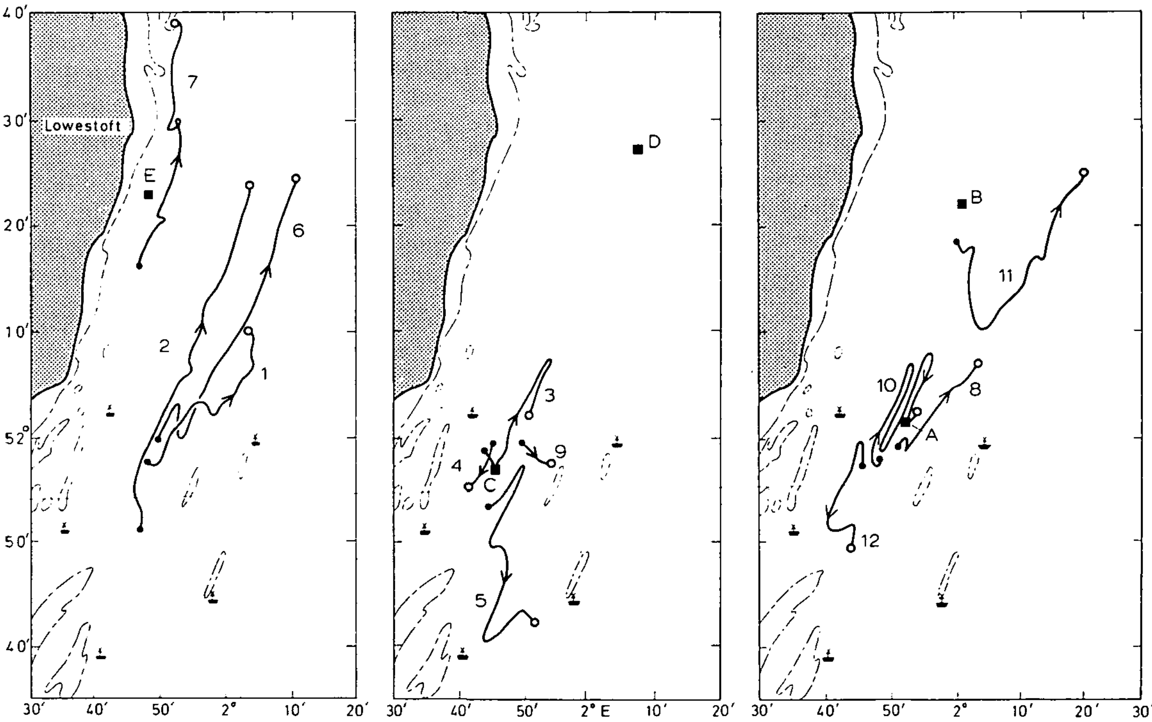

Figure 1. The tracks of 12 plaice fitted with acoustic transponding tags and followed by sector scanning sonar. Solid circle, start of track; clear circle, end of track. The 10 m depth contour and the positions of certain light-vessels are shown. The black squares mark the positions where current measurements were made: A, B, C and D, moored current meters; E, anchor station of RV "Corella" 13 December 1971.

screened from direct sunlight by day and deck lights by night.

The plaice were not fed at sea. Some of the fish swam freely about the tanks at night but during the day they were all buried in the sand, and a few were so deeply buried as to pass undetected until they were dug out at the end of the cruise. The fish did not suffer from the abrasions sometimes found on plaice held in sand-free tanks in conventional tagging experiments and there were no deaths among the 56 tagged plaice carried on the tracking cruises.

Working area

The fish were released and tracked off the East Anglian coast within an area bounded by the latitudes 51°40′N and 52°40′N (Harwich to Lowestoft) and the longitudes 1°40′E and 2°30′E and covered by Decca chain 5B/MP (English). As shown in Figure 1, many of the fish were released between the Shipwash and the Inner Gabbard banks where the depth of water varies from 22 m to 40 m (British Admiralty chart 1504). Admiralty Tidal Stations show that the tides run 013° and 180°, and 032° and 207°; in the northern and southern parts of the working area respectively[2], with speeds up to 140 cm s^{-1} at springs and a tidal range up to 3 m. The tide floods on the south-going stream. The bottom deposits in the area are mainly fine to medium sand (Jarke, 1956) with beds of gravel. Sector scanner observations (unpublished) show that there are areas where the bottom is covered by patches of sandwaves (wavelength approximately 2–3 m) lying normal to the tidal axis. The water in the area is relatively turbid and divers' observations indicate that even under good conditions visibility is limited to a few metres. During the day, and under conditions similar to those under which many of the fish were tracked, a diver could first see the bottom when 3 to 4 m above it (B. H. Holford, personal communication).

Tracking technique

Greer Walker, Mitson and Storeton-West (1971) have described the use of a 300 kHz acoustic transponding tag and sector scanning sonar for following the movements of plaice in the open sea. The method followed in the present experiments was developed from these preliminary trials and is similar to that adopted for following a Woodhead seabed drifter (Harden Jones, Greer Walker and Arnold, 1973).

[2] All directions are given in °True.

The tag has been described by Mitson and Storeton-West (1971). It comprises an electro-acoustic transducer, an electronic transmitter-receiver and a mercury battery power supply housed in an oil filled polyethylene cylinder (1·0 cm diameter × 5·1 cm long). When insonified by the pulse from the sector scanner the tag transmits a 3 ms pulse at 300 kHz which is easily recognized on the sonar display as a bright rectangular target.

The tag weighs 3–4 g in sea water and has a drag coefficient $C_{Do} = 0{\cdot}6$, and would be expected to slow down a gliding plaice by 5 to 7%. An actively swimming fish of the same length would have to increase its power output by about 5% to compensate for the extra drag (Arnold and Holford, in press); it seems unlikely that the tag would impede the fish significantly.

Immediately before the release of a fish an acoustic tag was activated by a simple soldering and sealing operation and its performance checked. The deck tanks were then partly drained to make it easier to select a fish. The chosen plaice was carefully removed, loosely wrapped in a wet cloth which covered the head, and placed on the deck. Even the most lively fish lay still when handled in this way (cf cod, Harden Jones and Scholes, 1974, p. 260). The acoustic tag was attached by fine braided nylon cord to the upper eye of the retaining pin of the Petersen disc tag. As the acoustic tag was being attached to the fish RV "Clione" went slowly astern, so that as the fish was released the ship was gliding away from it. The plaice was dropped over the starboard side and usually located by the sector scanner within a few seconds.

The parameters of the ARL sector scanner (Voglis and Cook, 1966) and its installation on board RV "Clione" have alrea dybeen described (Mitson and Cook, 1971). The facility for azimuth (horizontal) scanning allows the tagged fish to be positioned relative to the ship while elevation (vertical) scanning provides information on depth of the fish. Following the method used when tracking a seabed drifter (Harden Jones et al, 1973) the range was estimated directly from the sonar display to the nearest 5 m, and the bearing, or depth in elevation scanning, to the nearest 1°. With most observations made at ranges between 100–170 m, the depth of the fish would be correct to within ± 1·0 m and ± 2·0 m at the shorter and longer ranges respectively. A distinction was made between the three positions *on the bottom*, *close to the bottom*, and *just off the bottom*. In the first position the acoustic tag signal came back from the bottom, in the second the signal was slightly above but contiguous with the bottom, and in the third position the signal was clearly separated from, but less than 1°, in elevation above the bottom. The category *just off the bottom* would therefore include fish which were 2 and 3 m above the bottom, at ranges of 100 m and 170 m respectively[3]. Some plaice came so close to the surface that the signal from the acoustic tag was above the midline of the receiver beam when the transducer was used in vertical mode at a tilt angle of 0°. These fish must have been swimming above the transducer and thus within 4 m of the surface. The position of these fish was recorded as *surface* and they were given a nominal depth of 2 m. The depth of a fish was regularly checked during a track and was always recorded every 15 min and more frequently – up to once every 2 min – when required.

A tagged plaice was kept under continual surveillance throughout the period of tracking, RV "Clione" maintaining station 100–350 m up or down tide of the fish depending on the directions of wind and tide. A telephone link between the sector scanner room and the bridge allowed the sonar operator to report the range and bearing of the target regularly, and generally not less than once a minute, so that the Officer-of-the-Watch could manoeuvre the ship to keep station relative to the target. Station-keeping was made easier by using the ship's Pleuger active rudder.

Checks were made during preliminary trials and during some tracks to see if the plaice were disturbed by the noise of the ship. Fish lying on or buried in the bottom did not move when RV "Clione" passed overhead, and fish in midwater did not alter course or change depth when the vessel was close by or when the main engines were rung "hard astern" almost over the fish. It seems unlikely that the proximity of the ship had any influence on the movements of the fish. Nevertheless, whenever possible RV "Clione" maintained station relative to the plaice at ranges greater than 200 m, and only closed to obtain range and bearing information for the 15 min fixes, or to get more frequent observations on the depth of the fish in the water column.

Details of the weather, including wind force and direction, sea state, swell, and cloud cover, were recorded regularly every hour. The direction of the tide and the time of slack water were also recorded by the Officer-of-the-Watch; the slackwater period was taken as the 60 min centred about the time of slack water. Notes were kept of the visibility of the sun, moon, and stars.

The track of the fish over the ground was reconstructed from its range and bearing relative to the ship which was positioned every $\frac{1}{4}$ h by reference to the Decca Navigator System, whose maximum variable day and night errors were $\pm$ 45 m and $\pm$ 90 m respectively (Anon, 1953). The tracks were plotted on enlargements of Admiralty chart L(D5) 1504 at a scale of 1 cm to 380 m.

The sonar display was recorded on 16 mm cine film, video-tape, and polaroid film when required. In the laboratory frame-by-frame analyses of selected sequences of film were made with a Specto 16 mm motion film analyser to obtain more detailed information on the movements of the fish. In some areas the regular sequences of sand waves provided fixed reference points to estimate the speed of the fish over the bottom.

As the transducer stabilization system was designed to counteract the ship's motion likely to be associated with wind strengths up to Force 6 (22–27 knots, 11–14 m s^{-1}) most tracks were made in fair weather. Very few observations were made in rough weather; exceptionally the track of fish 2 was continued through a period of Force 7 winds and fish 8 had to be abandoned in a following Force 9 gale, not on account of difficulty in tracking, but as a precaution to avoid the risk of damage to the equipment if the ship had to turn to dodge into a heavy sea.

Water current measurements

Observations on tidal currents were made for comparison with the movements and behaviour of the fish. RV "Clione" worked alone on cruises 2/71 and 7/71 (tracks 1 to 6) and tidal observations accompanying these tracks were limited to the direction of the tide and the times of slack water recorded by the Officer-of-the-Watch. On cruise 7/71 these observations were supplemented by tracking a Woodhead seabed drifter and a parachute drogue in midwater; the results have already been described (Harden Jones et al, 1973).

As the successive positions of a fish were known from the 15 min fixes, its velocity through the water could be estimated by vector analysis if the current was measured at the depth at which the fish was swimming. More detailed information on currents was therefore gathered on later cruises. On cruise 13/71 RV "Clione" was accompanied by RV "Corella" from which water current measurements were made with a Kelvin Hughes Direct Reading Current Meter (DRCM) at an anchor station during track 7 (Fig. 1). For cruise 5/72, two recording current meter rigs were moored along the line of the tide at positions 52°01·5′N 01°52·3′E (rig A) and 52°22·0′N 02°01·0′E (rig B) (Fig. 1). The depths at the two stations were 38 m and 28 m respectively and

[3] Mr Holford's observations (p. 60) suggest that fish in the category *just off the bottom* would have been able to see the bottom during the day.

the meters were set to lie 16 m above the bottom. The fish were released at positions from which their tracks were expected to pass close to the meters. Figure 1 shows that tracks 8 and 10, and 11 and 12, were near rigs A and B respectively. Unfortunately rig A was run down by an unknown vessel during track 10 and while the meter was subsequently recovered in the English Channel, all the tidal data were lost.

As there was no satisfactory basis for extrapolating the tidal data recorded by the northern meter to the position of the southern meter, a further two rigs were moored along the tidal axis (rig C, 51°56·9′N 01°45·5′E; rig D, 52°27·3′N 02°07·4′E) for one tidal cycle on 14/15 August 1973. Each rig carried two current meters, one 9 m below the surface, the other 6 m above the bottom. The data from these stations have been analysed by Ramster and Medler (1978). At low tidal speeds the variation in speed and direction was high so that measurements have only been compared between the two stations when the current speed at either station exceeded 70 cm s^{-1}. The mean difference recorded on a northerly tide between the two upper meters was 0·6 ± 6·2 cm s^{-1} in speed and 12·6° ± 8·6° in direction.

The speed and direction through the water of fish 8, 10, 11 and 12 were calculated from vector diagrams for periods when the tidal speed exceeded 70 cm s^{-1}. The vector diagrams were constructed from the resultant vector of the fish over the ground and the tidal vector for the same 15 min period. To allow for the distance of the fish from current meter B a correction was made to the direction of the tide recorded by the meter on this rig. The correction was +0·71° and +0·44° per nautical mile to the south of the rig from the first and second halves respectively of each northerly tide. No correction was made to the speed of the tide as recorded by the meter.

During track 7 the DRCM was raised from 2 m to 14 m above the bottom as the fish moved from the bottom up into midwater. The fish was close to the DRCM during the single northerly tide on which observations were made so that no corrections were applied to the current measurements.

Results

In 1971 and 1972 RV "Clione" was available for four tracking cruises during which 12 plaice were released and followed off the East Anglian coast. Details of

Table 1. Summary of details relating to the release of plaice fitted with acoustic transponding tags and tracked in East Anglian waters during the period February 1971–April 1972

No.	Plaice L (cm)	Plaice W (g)	Sex	Release Date 1971/72	Release Time GMT	Direction of tide on release north, south or slack	Release position	Final position	Overall movement °True	km	h
1	45	–	F	20 Feb 1971	1317	S	51°57·8′N 1°47·2′E	52°10·0′N 2°03·6′E	035°	29	25
2	44	–	F	9 Jun 1971	1250	N	51°51·4′N 1°46·5′E	52°24·0′N 2°04·0′E	017°	61	44
3	37	–	F	17 Jun 1971	0010	LWS	51°58·9′N 1°44·4′E	52°02·2′N 1°51·4′E	044°	9	38
4	42	–	M	19 Jun 1971	1430	LWS	51°59·1′N 1°45·5′E	51°55·2′N 1°41·2′E	210°	9	5
5	37	–	F	19 Jun 1971	2015	HWS	51°53·1′N 1°44·4′E	51°42·0′N 1°52·0′E	157°	23	34
6	37	–	F	24 Jun 1971	1644	N	51°59·7′N 1°48·6′E	52°24·4′N 2°10·8′E	028°	43	54
7	41	604	F	12 Dec 1971	1009	N	52°16·5′N 1°46·3′E	52°39·0′N 1°52·3′E	009°	43	26
8	39	450	F	9 Apr 1972	1152	N	51°59·1′N 1°51·2′E	52°07·2′N 2°03·3′E	045°	21	22
9	44	665	F	11 Apr 1972	2103	S	51°59·3′N 1°49·4′E	51°57·3′N 1°54·0′E	114°	6	27
10	42	668	M	13 Apr 1972	2136	S	51°58·0′N 1°48·4′E	52°02·4′N 1°53·7′E	038°	11	27
11	52	1 133	F	17 Apr 1972	1029	S	52°18·8′N 2°00·1′E	52°25·9′N 2°20·5′E	062°	26	36
12	36	478	M	20 Apr 1972	1708	N	51°57·5′N 1°45·7′E	51°49·4′N 1°44·0′E	187°	16	20

the fish are given in Table 1 and an overall summary of the tracks is shown in Figure 1. The tag attached to fish 4 failed 5 h after release. Of the other 11 fish, 8 moved a point-to-point distance of more than 15 km from the release position to that at which the track ended: 6 of the fish (1, 2, 6, 7, 8 and 11) moved north and 2 fish (5 and 12) moved south. These 8 fish showed a consistent pattern of selective tidal stream transport which was not evident in the tracks of the remaining 3 fish (3, 9 and 10) which moved point-to-point distances of 9, 6 and 11 km respectively.

Fish that moved more than 15 km

The fish made regular vertical migrations, and they came off the bottom at or near slack water and re-

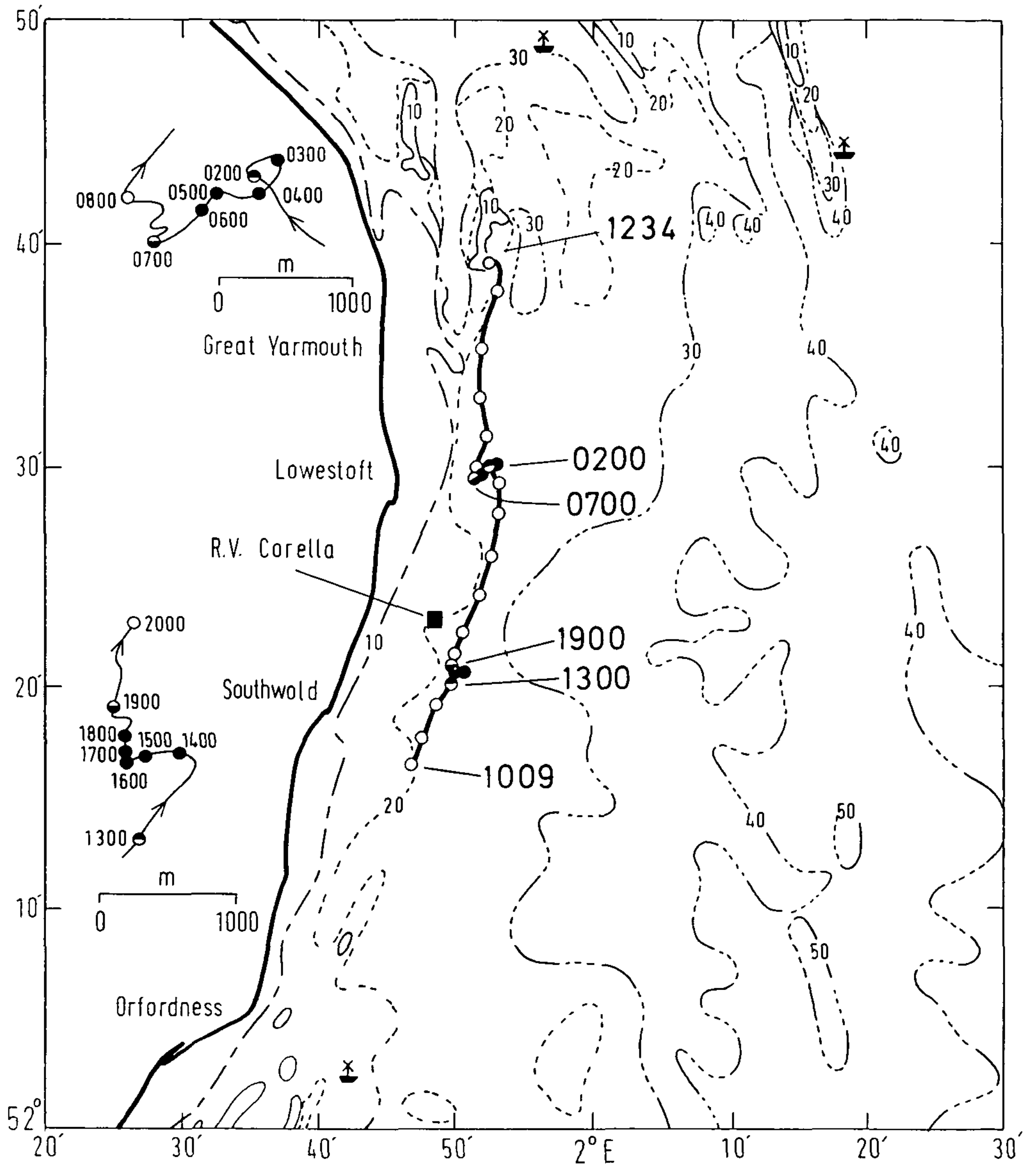

Figure 2. Track chart of plaice 7, released at 1009 h, 12 Dec 1971. Hourly positions of the fish are indicated and the times of slack water are given. O north-going tide, low water slack, ● south-going tide, high water slack. The insert figures on the land show details of the track during the south-going tides at the scale indicated. The position of RV "Corella's" anchor station is shown. Depth contours in metres (the depth contours in this and other figures are taken from the North Sea Fisheries charts L(D5) 5201 and 5100).

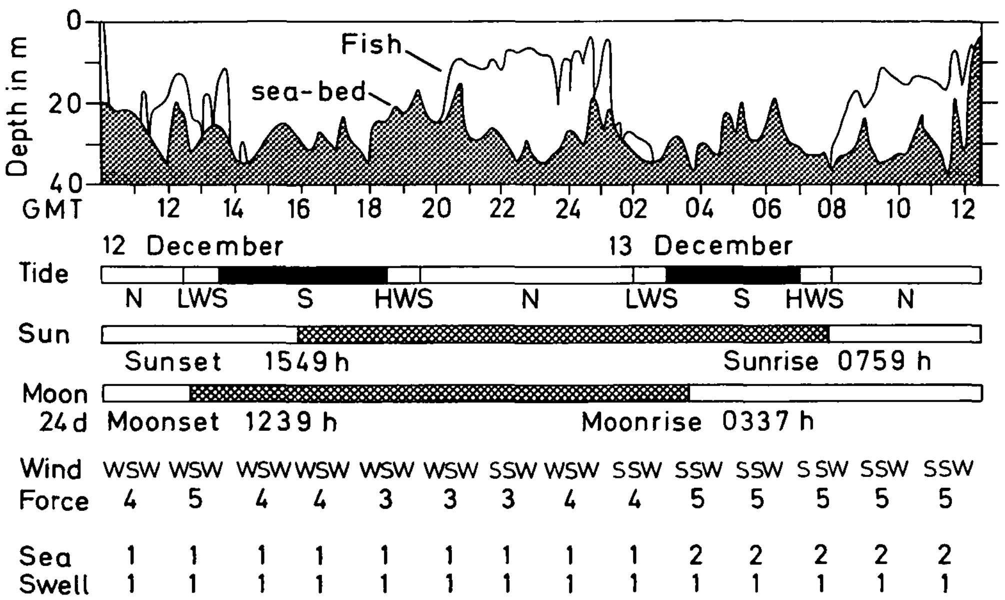

Figure 3. The depth of plaice 7 in relation to the direction of the tide and other environmental factors.

mained in midwater for the following 5–6 h before returning to the bottom. When in midwater the fish moved downstream with the tide for a distance of 12–16 km, more or less equal to that of the tidal displacement.

Activity appeared to be greatly reduced when a fish was on the bottom; some fish did not move for 2–3 h. The regular cycle of movements on and off the bottom at slack water was very striking and the 12 h period justified their description as semi-diurnal vertical migrations. The semi-diurnal pattern was characteristic of the tracks of the fish which moved 15 km or more during the period of surveillance. A description of the track of plaice 7 will be given as a typical example. Exceptionally, fish 2 showed a diurnal rhythm of vertical migration and the track of this fish is also described in detail.

Tracks of individual fish

The track of plaice 7. (Track chart, Fig. 2; vertical movements, Fig. 3). Plaice 7 was released on 12 December 1971 at a position 24 km NE × N of Orfordness and tracked for 26½ h before it was abandoned 43 km to the north when it moved into shallow water. During the track current measurements were made from RV "Corella" using a DRCM. Details of the track, the depth of the fish, and the relevant environmental factors are summarized in Figures 2 and 3.

The fish was released at 1009 h on a northerly tide and reached the bottom after 6 min, returning to midwater an hour later. The fish stayed in midwater for the rest of the northerly tide and made 4 excursions to the bottom (at 1130 h, 1302 h, 1320 h and 1325 h) before finally settling at 1355 h (low water slack 1230–1330 h). Between release and the end of the north-going tide the fish went 6·69 km to the north-east at an average ground speed of 79 cm s^{-1}. During the southerly tide the fish stayed on or close to the bottom and never moved into midwater. It swam slowly over or along the sandwaves with frequent changes in direction, moving overall 1·80 km to the northwest at an average ground speed of 7 cm s^{-1}; there was no change in activity or depth related to sunset at 1549 h. Activity increased at slack water (high water slack 1830–1930 h) and the fish came clear of the bottom – category *just off bottom* – at 2000 h and moved into midwater at 2015 h. The tide had just turned to run to the north, water current measurements made on board RV "Corella" indicating a velocity of 19 cm s^{-1}, 009°T, at a height of 2 m above the bottom. From 2200–2330 h the fish was high in the water column and often within 10 m of the surface. There was no moon and the stars were not visible through a cloudy sky. After two preliminary excursions (0055 h and 0125 h) the fish returned to the bottom at 0235 h (low water slack 0200–0300 h). When in midwater from 2015–0200 h the fish covered 18·42 km over the ground at

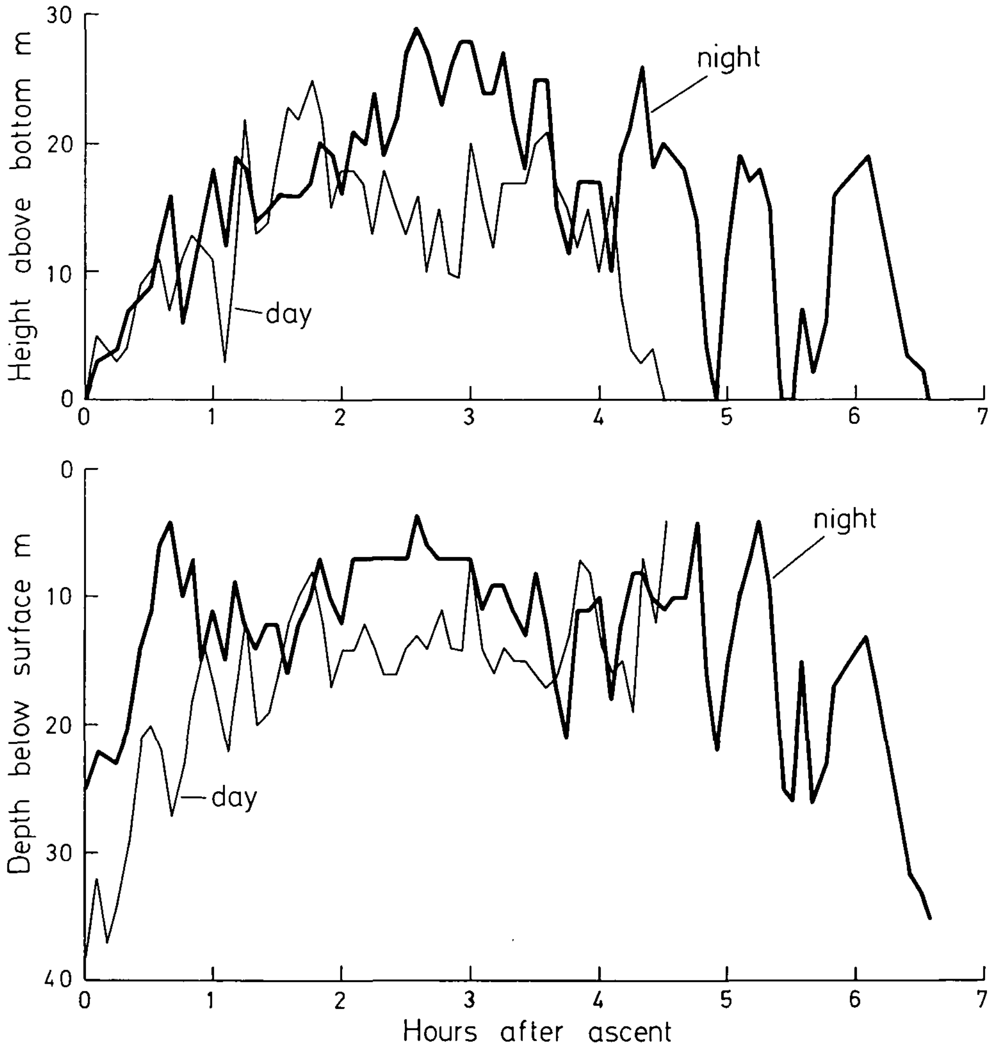

Figure 4. The height above the bottom and depth below the surface of plaice 7 when in midwater on a northerly tide by night (2000–0235 h, 12/13 Dec) and by day (0800–1234 h, 13 Dec).

an average speed of 97 cm s^{-1}. The fish stayed on the bottom throughout the south-going tide and followed a twisted path to cover 1·20 km to the south-west at an average speed of 8 cm s^{-1}. The fish was only once recorded as being *just off bottom*, and then for only 1 min at 0645 h. The fish left the bottom at 0800 h (sunrise 0759 h) and swam straight into midwater. Low water slack was within the period 0700–0800 h and when the fish "took-off" measurements made from RV "Corella" indicated a current velocity of 15 cm s^{-1}, 030°T, at a height of 2 m above the bottom. The fish stayed in midwater during the northerly tide and covered 18·70 km over the ground at an average speed of 114 cm s^{-1} before moving into shallow water at the Cross Sand where the track ended. As indicated in Figure 3, the weather during the track was reasonably good. The sun was not

Table 2. Plaice 7. Height above the bottom and depth below the surface when in midwater by day and by night. Depths recorded at ¼ h observations for hours 2, 3 and 4 after ascent

	Height above the bottom in m		Depth below the surface in m	
	Day	Night	Day	Night
n	36	36	36	36
$\bar{x}$	15·9	20·4	14·0	10·1
s.d.	4·5	4·8	3·3	3·5
t	4·114***		4·714***	

visible on 12 December but was seen on 13 December.

Plaice 7 gained ground to the north during the northerly tide, leaving the bottom for midwater just after high water slack and returning to the bottom at low water slack or just after the tide had turned south. These vertical movements were clearly related to the tidal cycle. The final descent from midwater onto the bottom was preceded by several brief excursions (see Fig. 3, 2400–0200 h), the fish swimming down close to and apparently resting on the bottom for about 1–2 min before returning to midwater. The rates of descent and ascent in these movements ranged from 0·83 to 2·50 m min^{-1}.

Plaice 7 was in midwater for two north-going tides, the first during the night and the second during the day. Figure 4 shows that the fish was both higher off the bottom and closer to the surface during the night than during the day. The differences were significant (Table 2).

Data on the direction and speed of plaice 7 over the ground are summarized in Table 3. Reference to this table and Figure 2 shows that the ground speed was low and the track twisted when the fish was on the bottom. But the ground speed was high and the track straight when the fish was in midwater. The tide was then set in the direction of overall movement which was, for this fish, to the north.

From 2230–0130 h water current measurements were made from RV "Corella" at a depth of 10 m when the fish was swimming in midwater. During this period the distance between the fish and RV "Corella"'s anchor station increased from 6 km to 15 km. From these measurements and observations the velocity of the fish through the water was estimated by vector analysis. The results are set out in Table 4 and shown in Figure 5. From 2230–0130 h the fish moved north at speeds through the water with the range 39–85 cm s^{-1} (0·9–2·0 body lengths (L) s^{-1}), and was therefore swimming, and presumably heading, downstream in the same general direction of the tide. The movements of the fish became more variable towards the end of the northerly tide and there were two brief excursions to the bottom, at 0055 h and 0125 h, as indicated in Figures 3 and 5. By 0045 h the tidal current as measured at

Table 3. Plaice 7. The relation between tidal direction, position in the water column, distance and direction moved, and speed over the ground

Observation period	Time GMT	Direction of tide	Position and movement of fish: Position in water column	Distance moved in km	Course over ground in °True	Speed over ground cm s^{-1}
1	1009–1230	north	in midwater	6·69	024°	79
2	1330–1830	south	on bottom	1·80	355°	10
3	2015–0200	north	in midwater	18·42	010°	89
4	0300–0700	south	on bottom	1·20	237°	8
5	0800–1234	north	in midwater	18·70	004°	114

Table 4. Plaice 7. Water velocity (from DRCM observations), fish velocity over the ground (from successive ¼ h fixes), and fish velocity through the water (from vector analysis). From 2230–0130 h 12–13 December 1971

Time GMT	Water velocity from current meter °True	cm s^{-1}	Fish velocity over the ground °True	cm s^{-1}	Fish velocity through the water °True	cm s^{-1}
2230–2245	029°	69	013°	100	345°	39
2245–2300	025°	64	040°	132	055°	73
2300–2315	021°	62	019°	108	016°	46
2315–2330	023°	60	334°	111	302°	84
2330–2345	022°	55	013°	89	360°	36
2345–2400	022°	54	006°	89	345°	40
2400–0015	024°	54	030°	126	034°	73
0015–0030	026°	47	325°	98	297°	85
0030–0045	026°	39	306°	79	278°	82
0045–0100	026°	32	021°	66	018°	35
0100–0115	032°	27	037°	82	039°	55
0115–0130	017°	20	297°	49	274°	49

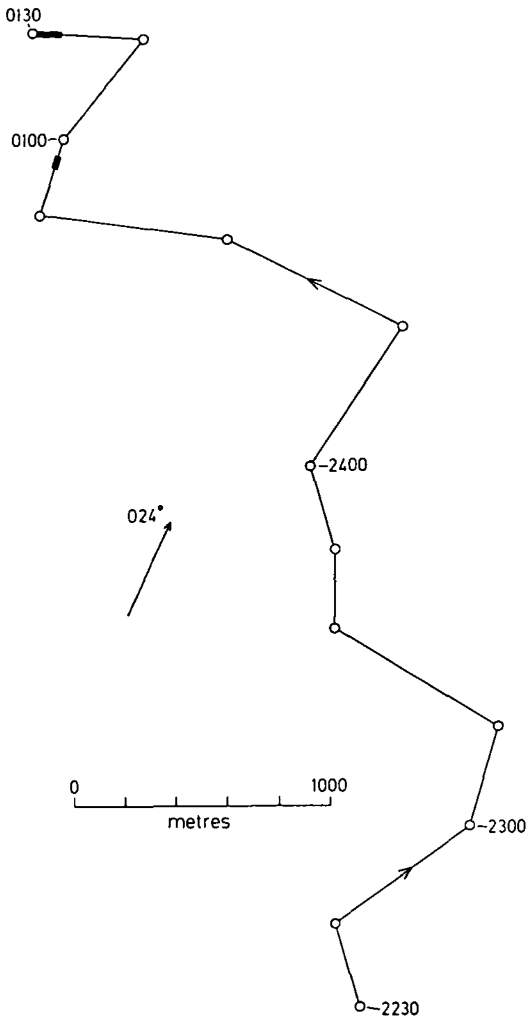

Figure 5. Progressive vector diagram to show the movement of plaice 7 through the water (from data summarised in Table 4). Positions are shown at each ½ h. The thickened parts of the track at 0055 h and 0125 h indicate periods when the fish made excursions to the bottom (see Fig. 3). The direction of the tide is shown.

RV "Corella"s anchor station had fallen below the level at which reliable measurements could be made.

The track of plaice 2. (Track chart, Fig. 6; vertical movements, Fig. 7). Plaice 2 was released at 1250 h on 9 June 1971 at a position 30 km SE of Orfordness. The tide was running north and the fish went straight to the bottom at a depth of 44 m, but soon returned to midwater before settling on the bottom at 1345 h. During the remaining 3¼ h of the northerly tide the fish moved 6·23 km north at a ground speed of 53 cm s^{-1}. After slack water (1700–1800 h) the northerly movement continued at a slower ground speed against the southerly tide. From 1800–2400 h the fish moved 3·0 km at a mean speed of 14 cm s^{-1}, and during the next slackwater period (2400–0100) h came off the bottom at 0015 h and stayed in midwater for 2¾ h. Following one excursion at 0247 h (see Fig. 7) the fish settled on the bottom at 0300 h (sunrise 0341 h). When in midwater from 0100–0300 h the fish moved north with the tide for 8·9 km at a speed of 124 cm s^{-1}. The fish continued north when on the bottom and from 0300 h until the next slack (0600–0700 h) and covered 6·3 km over the ground at a speed of 59 cm s^{-1}. The fish stayed on the bottom through the next southerly tide, and continued to move to the north but at a greatly reduced speed; from 0700–0815 h it covered 0·4 km at a ground speed of 9 cm s^{-1}. The fish did not appear to move from 0815–1145 h: slack water was within the period 1200–1300 h. At 1200 h the fish started to move north and keeping on the bottom covered 13·4 km from 1200–1800 h at a speed of 62 cm s^{-1}. After the next slack water (1800–1900 h) the fish stayed on the bottom during the south-going tide and did not move between 1845 h and 2330 h. Movement to the north recommenced towards the end of the southerly tide, and between 2330 h and 2400 h the fish covered 285 m at a ground speed of 15 cm s^{-1}. Slack water was within the period 2400–0100 h and the fish came off the bottom into midwater at 0008 h to join the northerly tide. With the exception of an excursion to the bottom at 0530 h, the fish stayed in midwater until 0615 h, when it returned to the bottom shortly before slack water at 0700–0800 h. When in midwater the fish covered 20·5 km over the ground at a speed of 95 cm s^{-1}. The fish did not appear to move after returning to the bottom at 0615 h. The signal from the acoustic tag weakened soon after midnight and contact with the fish was finally lost at 0830 h.

Plaice 2 was tracked for 44 h. During this period it moved 61 km to the north at a speed of 39 cm s^{-1}, 0·9 L s^{-1}. Plaice 2 only came into midwater to join the northerly tide at night and moved to the north when on the bottom during both northerly and southerly tides. Table 5 summarizes the relation between tide, position in the water column, distance moved and speed over the ground. There were three periods when this fish moved north against a south-going tide (Table 5, periods 2, 5 and 9). While periods 5 and 9 were short and towards the end of the south-going tide, the northerly movement during period 2 was maintained throughout much of the south-going tide. The insert in Figure 6 shows that little ground was gained against the tide between 1900 h and 2200 h when its velocity would have been greatest. The fish

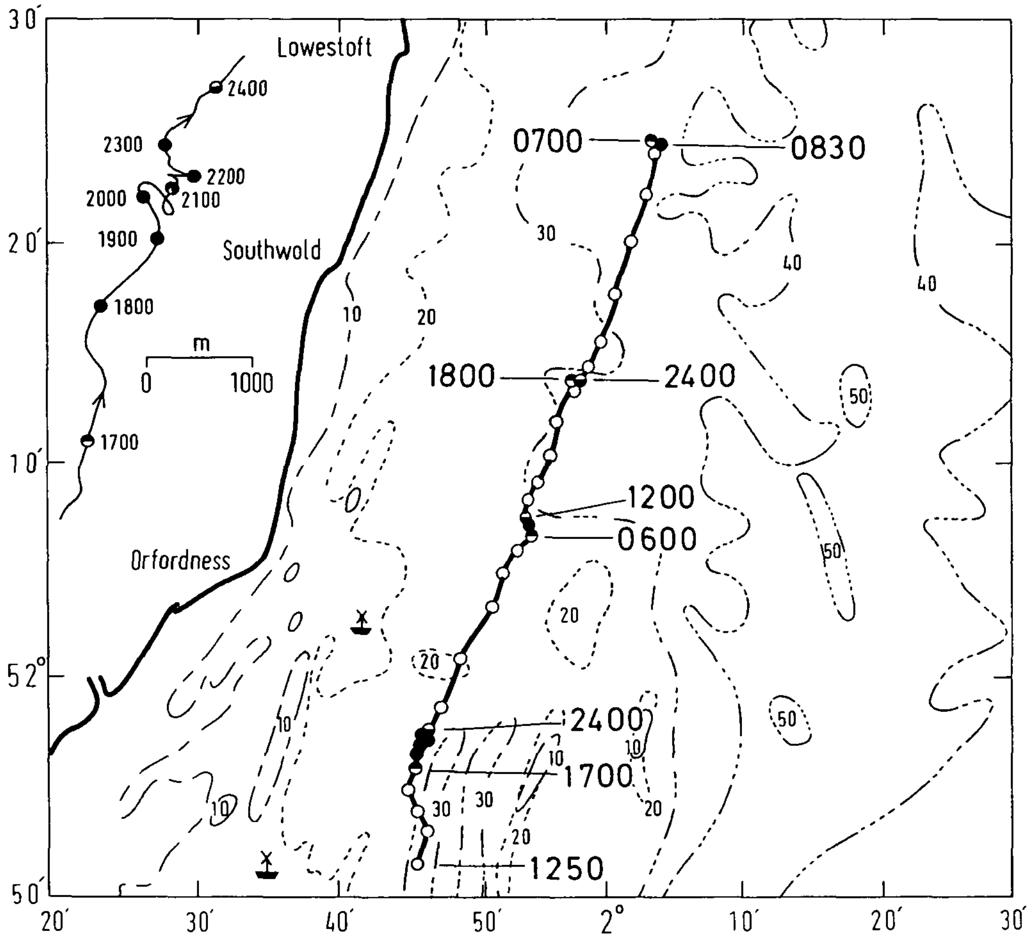

Figure 6. Track chart of plaice 2 released at 1250 h, 9 June 1971. Hourly positions of the fish are indicated and the times of slack water are given. ○ north-going tide, ◓ low water slack, ● south-going tide, ◒ high water slack. The insert figure on the land shows details of the contranatant movement on the bottom during the period 1700 h to 2400 h. Sunset was at 2018 h. Depth contours in metres.

was on the bottom and its movement could be described as contranatant. Although the overall movement of plaice 2 was to the north, the fish was on the bottom for all of one (period 7) and for part of two (periods 1 and 4) northerly tides. Its speed over the ground on northerly tides was slower when on the bottom (53, 59 and 62 cm s^{-1}) than when in midwater (124 and 95 cm s^{-1}). The contrast is particularly marked when comparing the speed over the ground during periods 3 and 4. The movement off the bottom at 0015 h on 10 June and the failure to leave the bottom during the next northerly tide at 1300 h, suggests a diurnal (24 h period) rhythm. The sky was overcast during the track and the sun was not visible on 10 June. The day was one of increasing northerly winds and swell, the wind reaching Force 7 by 1300 h.

Main features of the tracks

Behaviour soon after release

The conditions on release are summarised in Table 6. Plaice 1, 2 and 5 reached the bottom within 1 min of release; plaice 7, 8, 11 and 12 reached the bottom within 3–6 min; and plaice 6 stayed in midwater for over 3 h. Plaice 7, 8 and 12 (all released on northerly tides) soon returned to midwater after short periods on the bottom (15, 3 and 12 min respectively) but

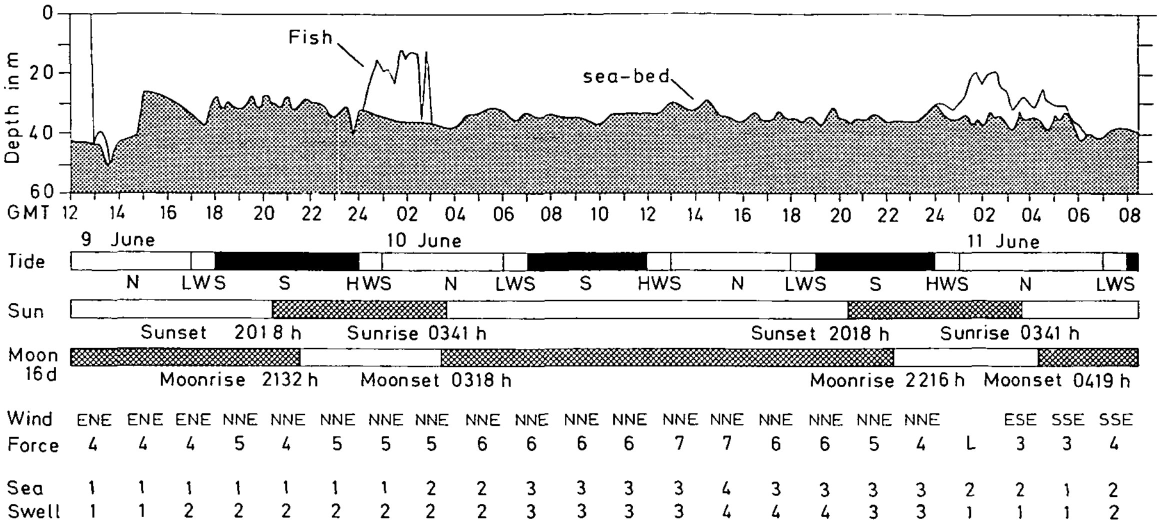

Figure 7. The depth of plaice 2 in relation to the direction of the tide and other environmental factors.

Table 5. Plaice 2. The relation between tidal direction, position in the water column, distance and direction moved and speed over the ground

Observation period	Time GMT	Direction of tide	Position and movement of fish: Position in water column	Distance moved in km	Course over ground in °True	Speed over ground cm s^{-1}
1	1345–1700	north	on bottom	6·23	354°	53
2	1800–2400	south	on bottom	3·08	021°	14
3	0100–0300	north	in midwater	8·90	025°	124
4	0300–0600	north	on bottom	6·35	030°	59
5	0700–0815	south	on bottom	0·40	323°	9
6	0845–1145	south	on bottom	0·00	–	–
7	1200–1800	north	on bottom	13·45	019°	62
8	1900–2330	south	on bottom	0·00	–	–
9	2330–2400	south	on bottom	0·29	060°	16
10	0015–0615	north	in midwater	20·56	017°	95

Table 6. Plaice that moved more than 15 km during the period of surveillance: conditions at release and direction of overall movement

Fish	Conditions at release: Day or night	State of tide	Overall movement
1	day	south	north
2	day	north	north
5	dusk	HWS	south
6	day	north	north
7	day	north	north
8	day	north	north
11	day	south	north
12	day	north	south

plaice 2 – also released on a northerly tide – remained on the bottom for 11 h. Plaice 5, released at high water slack came off the bottom immediately and remained in midwater for the following northerly tide.

Both fish (plaice 1 and 11) released on southerly tides stayed on the bottom and moved south.

Time spent in midwater and ground speed

Selective tidal stream transport, associated with a semi-diurnal pattern of vertical migration, was – with the exception of plaice 2 – a feature of the tracks of all the fish which moved more than 15 km during the period of surveillance. Table 7 shows that the fish spent up to half their time in midwater, mainly on the tide whose direction coincided with that of their overall movement. Thus fish which moved north (plaice 1, 6, 7, 8 and 11) or south (plaice 5 and 12) were usually in midwater when the tide was running north or south respectively. Table 8 shows

Table 7. Plaice that moved more than 15 km during the period of surveillance: time spent in midwater, and proportion of time spent in midwater on northerly and southerly tides in relation to direction of overall movement. Values for the coincident tides are printed in bold type

Fish	Duration of track in min (a)	Overall direction north or south	Time in midwater min (b)	Time in midwater as % of (a)	Time in midwater as a percentage of (b) Northerly tide	Southerly tide	Slack water
1	1 490	north	780	52	**81**	5	14
2	2 616	north	581	22	**85**	0	15
5	2 025	south	1 095	54	41	**47**	12
6	3 270	north	1 335	41	**78**	9	13
7	1 575	north	830	53	**89**	0	11
8	1 335	north	744	56	**60**	8	32
11	2 160	north	750	35	**88**	0	12
12	1 216	south	570	47	29	**66**	5

Table 8. Plaice that moved more than 15 km during the period of surveillance: distance moved in km and ground speeds in cm s^{-1} when in midwater on northerly and southerly tides. Values for the coincident tides are printed in bold type

Fish	Overall direction of movement	Distance covered in km Northerly tide	Southerly tide	Ground speed in cm s^{-1} Northerly tide	Southerly tide
1	north	33·5	0·5	**86**	25
2	north	31·2	0·0	**106**	–
5	south	19·0	27·6	70	**90**
6	north	56·6	5·2	**91**	72
7	north	40·0	0·0	**91**	–
8	north	17·9	2·2	**66**	61
11	north	32·0	0·0	**81**	–
12	south	3·7	17·8	37	**79**

Table 9. Plaice that moved more than 15 km during the period of surveillance: average ground speeds for duration of track

Fish	Length in cm	Duration of track in min	Straight line distance between release and final positions in km	Speed over ground km h^{-1}	cm s^{-1}	$L\ s^{-1}$
1	45	1 490	29	1·17	32	0·71
2	44	2 616	61	1·40	39	0·88
5	37	2 025	23	0·68	19	0·51
6	37	3 270	43	0·79	22	0·59
7	41	1 575	43	1·64	46	1·11
8	39	1 335	21	0·94	26	0·67
11	52	2 160	26	0·72	20	0·38
12	36	1 216	16	0·79	22	0·61

Table 10. Plaice that moved more than 15 km during the period of surveillance: times of ascents and descents in relation to the slackwater period. The ascents are numbered 1–18 and the descents 19–37 in Figure 8

Vertical movement Category	Totals		Time of vertical movement in relation to slack water: Minutes before, more than 60	30 to 60	up to 30	Within slackwater period	Minutes after, up to 30	30 to 60	more than 60
Ascents	*n*	18	0	0	0	8	6	1	3
	%	100	–	–	–	44	33	6	17
Descents	*n*	19	3	1	1	7	1	3	3
	%	100	16	5	5	37	5	16	16

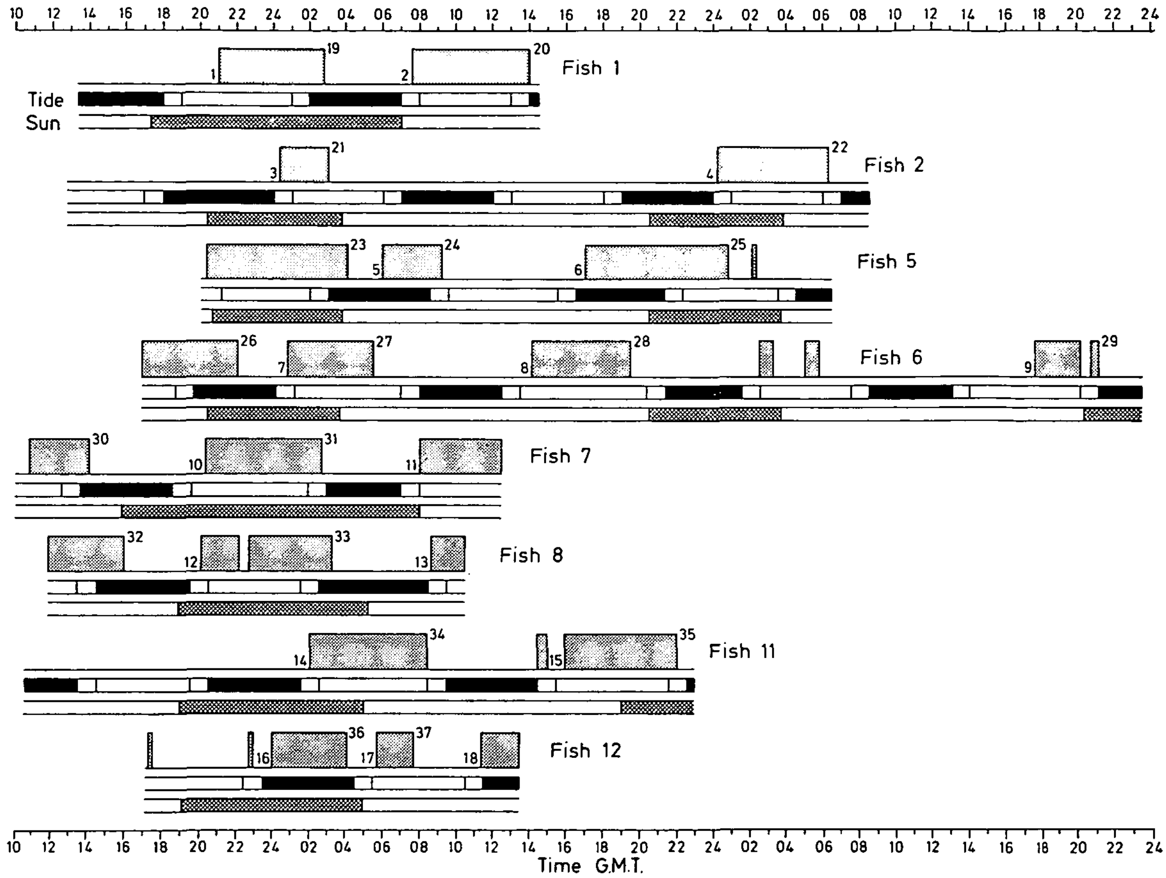

Figure 8. The timing of ascents and descents in relation to slack water for plaice which moved more than 15 km during the period of surveillance. The period in midwater is indicated by the stippled rectangles and ascents and descents are numbered 1 to 18 and 19 to 37 respectively. The duration of the south-going tide is shown by a black bar (followed by high water slack), and the duration of the north-going tide by a white bar (followed by low water slack).

that the fish covered most ground and had the highest ground speeds when in midwater on the coincident tide. The average ground speeds, calculated from the straight line distance between release and final positions and duration of the track, are summarized in Table 9. The average ground speeds ranged from 0·68 to 1·64 km h^{-1}, 19 to 46 cm s^{-1}, or, in terms of fish lengths, from 0·38 to 1·11 L s^{-1}.

Ascents and descents

The movements off or onto the bottom were related to slack water and Table 10 summarises the data for 18 ascents and 19 descents (numbered 1–18 and 19–37 respectively in Fig. 8) which preceded extended (1 h or more) periods in midwater or on the bottom. There was no significant difference between the speeds at which plaice moved up or down the water column, the mean of 29 displacements involving depths of 10 m or more being 1·3 $\pm$ 0·6 m min^{-1}.

Fish which had been lying on the bottom with little or no movement usually became more active at slack water. After crossing several sandwaves while on the bottom, some fish then moved directly into midwater, (Fig. 9, plaice 6, ascent 8); others swam for some distance 1–2 m above the bottom (category *just off the bottom*) and "took-off" after one or more preliminary "hops" (Fig. 9, plaice 12, ascent 16). Some fish which went into midwater half way through the slackwater period showed a clear increase in activity before leaving the bottom: two examples are given in Table 11.

Ascents appeared to be more closely associated with slack water than descents, 77% of the former being within $\pm$ 30 min of the slackwater period as compared with 47% of the latter. No ascents were made before the slackwater period. Most descents were preceeded by excursions to the bottom. These

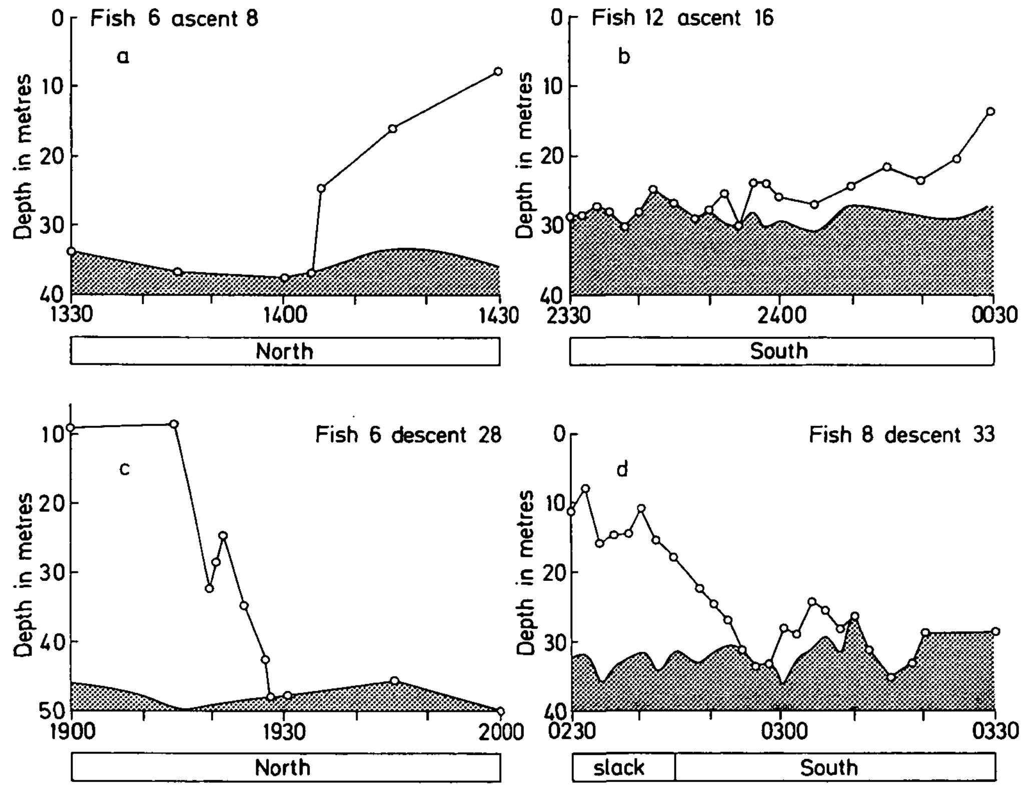

Figure 9. Selected ascents and descents. a, ascent without a preliminary "hop"; b, ascent with a preliminary "hop"; c, descent without a preliminary excursion to the bottom; d, descent with a preliminary excursion to the bottom. The state of the tide is indicated.

movements were usually made during the last 2–3 h of a 5 h period in midwater, and the fish would stay on the bottom for 1–5 min before returning to midwater. Excursions were observed during the track of plaice 7 (see Fig. 3) and another example is shown in Figure 9 (plaice 8, descent 33). But some descents (numbers 24, 25 and 28) were made without any preliminary excursion. One fish was described in the track log as having "fallen out of the water"; this particular descent (plaice 6, descent 28) is shown in Figure 9. Table 12 summarises the data available for the descents numbered 19–37 in Figure 8. No single factor appears to be related to the match or mismatch between the descents and the time of slack water. Thus the seven descents made within the slackwater period were preceeded by a variable number of excursions (0 to 3) and were made by day or night under a range of sea conditions with wind strengths ranging from light airs (descent 34) to Force 6 (descent 5). While plaice 11 made two descents within the slackwater period, and plaice 8 two descents well outside it, others (for example plaice 5 and 6) made descents within and without the slackwater period. The geographical position of the descents did not suggest that there were particular areas associated with the two types of movements.

Height above the bottom and depth below the surface

Plaice 7 was higher off the bottom and closer to the surface during the night than during the day (p. 66) but a similar difference was not evident in the tracks of other plaice. The pooled data for all ¼ h observations (excluding those made during the first hour after ascent when the fish were approaching a steady level, and movements clearly associated with excursions to the bottom) are summarised in Tables 13 and 14. There was no significant difference between the depth below the surface or the height above the bottom by day and by night. Figure 10 shows that when off the bottom plaice usually swam just above the middle of the water column.

The data were examined for any relation between the depth of the fish when in midwater and the

Table 11. Increase in activity at slack water before moving into midwater

Fish	Ascent	Tide	Position of fish in water column	Period of observation in min	Distance moved in km	Mean ground speed cm s^{-1}
1	2	south	on bottom	280	3·54	21
		slack	on bottom	20	0·50	42
		slack	in midwater	40	1·70	71
		north	in midwater	317	18·94	100
2	4	south	on bottom	314	0·33	2
		slack	on bottom	30	0·30	17
		slack	in midwater	30	1·02	57
		north	in midwater	345	20·32	98

Table 12. Plaice that moved more than 15 km during the period of surveillance: the timing of a descent in relation to the next slackwater period following a vertical movement into midwater. The numbering of the descents 19–37 follows that given in Figure 8. The number of preliminary excursions and other relevant factors are also given

Fish	Time of descent in relation to the slackwater period: Within slackwater period					30 min before or after					30–60 min before or after					More than 60 min before or after				
	descent number	number of excursions	tidal direction north (N) or south (S) when left bottom or in midwater	day (d) or night (n) descent	wind Force	descent number	number of excursions	tidal direction north (N) or south (S) when left bottom or in midwater	day (d) or night (n) descent	wind Force	descent number	number of excursions	tidal direction north (N) or south (S) when left bottom or in midwater	day (d) or night (n) descent	wind Force	descent number	number of excursions	tidal direction north (N) or south (S) when left bottom or in midwater	day (d) or night (n) descent	wind Force
1	20	2	N	d	5	19	2	N	n	4	–	–	–	–	–	–	–	–	–	–
2	22	1	N	d	3	–	–	–	–	–	–	–	–	–	–	21	1	N	n	5
5	24	0	S	d	6	–	–	–	–	–	23	6	N	d	6	25	0	S	n	3
6	29	1	N	n	5	–	–	–	–	–	28	0	N	d	4	26	2	N	n	4
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27	?	N	d	3
7	31	2	N	d	5	30	4	N	d	4	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	33	4	N	n	5	32	1	N	d	3
11	34	4	N	d	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	35	2	N	n	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	36	1	S	n	5	–	–	–	–	–	37	3	S	d	5

weather as measured by the sea state (WMO Code 75). Table 15 shows that plaice swam within 5m of the surface up to sea state 3 (wave heights up to $1\frac{1}{4}$ m). Fish tracking is fair weather work (p. 61) and only 13 observations were made in sea states 4 and 5: in each instance the fish were at depths of 20 m or more.

Orientation

As deduced from movement over the ground. The data were examined for any evidence that the fish were orientated to the tidal stream during the tracks. Fish heading upstream and gaining ground against the tide – that is swimming contranatantly in the classical sense (Harden Jones, 1968, p. 15) – would be expected to move over the ground at angles of more than 90° to the left or right of the direction of the tide. The direction of movement over the ground in °True between successive $\frac{1}{4}$ h fixes was measured on the large scale plots and the results are summarised in Table 16. Out of a total of 639 observations, 72 were consistent with fish gaining ground against the tide. All these movements against the tide were made when the fish were on the bottom: no contranatant movements were recorded when the fish were in midwater.

Inspection of the track charts showed that fish moving against the tide rarely covered more than 200–300 m between 15 min fixes (average ground speed about 30 cm s^{-1}) and that it was unusual for contranatant behaviour to be maintained for more than 30 min. Plaice 2 was an exception and was the

Table 13. Plaice that moved more than 15 km during the period of surveillance: mean height above the bottom in m. Data from observations made every ½ h when the fish were in midwater excluding those made in the first hour after ascent and movements clearly associated with excursions to the bottom

	Day		Night
n	96		107
$\bar{x}$	19·68		18·42
s.d.	10·35		8·36
t		0·945	
$t_{0.05}$		1·960	

Table 14. Plaice that moved more than 15 km during the period of surveillance: mean depths below the surface in m. Data from observations made every ½ h when the fish were in midwater excluding those made in the first hour after ascent and movements clearly associated with excursions to the bottom

	Day		Night
n	96		107
$\bar{x}$	17·36		15·87
s.d.	12·11		11·14
t		0·906	
$t_{0.05}$		1·960	

only plaice to gain ground consistently against the tide; its track has already been described in detail.

As deduced from movement through the water. The direction of movement over the ground does not give any information about the orientation of a fish in midwater moving downstream with the tide. But if the ground speed of the fish was so fast or so slow as to be clearly inconsistent with passive drift, the fish must be actively swimming, and presumably heading, with or against the tide respectively. For

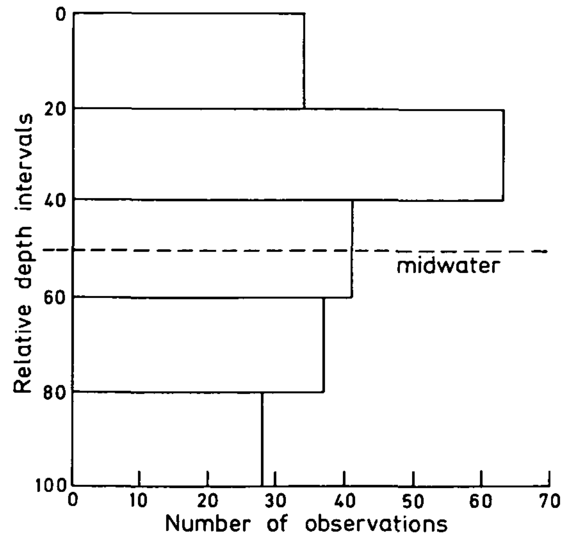

Figure 10. Depth of plaice when in midwater expressed as a proportion of the total depth of water. The number of observations are shown at 20% depth intervals. Total number of observations 203.

example, during the track of plaice 7, the Master commented that he had to use RV "Clione"s main engines – rather than the Pleuger rudder – to maintain contact. Current meter observations were made from RV "Corella" during this track and vector analysis (p. 66) showed that for a 2 h period plaice 7 was apparently swimming and heading in a northerly direction when in midwater on the north-going tide.

Plaice 8 and 11 both moved north and came within the area covered by the current meters A and B (see Fig. 11). Progressive vector diagrams were constructed for those portions of their tracks when the tidal current exceeded 70 cm s^{-1}, using the corrections detailed earlier (p. 62). Plaice 8 (Fig. 11a) swam through the water on a course of about 110°T for 1½ h (2236–0015 h) when in midwater at night under

Table 15. Plaice that moved more than 15 km during the period of surveillance: number of observations made at ½ h intervals of fish at different depths below the surface, grouped by four range categories, at different sea states (WMO Code 75)

Depth range in m	Observations at different sea states 1		2		3		4		5	
	n	%	n	%	n	%	n	%	n	%
0·0– 4·9	8	11	15	19	6	15	0	0	0	0
5·0– 9·9	17	24	15	19	7	18	0	0	0	0
10·0–19·9	20	28	26	32	15	39	0	0	0	0
over 20	26	37	24	30	11	28	9	100	4	100
Totals	71	100	80	100	39	100	9	100	4	100

Table 16. Plaice that moved more than 15 km during the period of surveillance: summary table to show the occurrence of movements consistent with contranatant behaviour. For further details see text

Fish	Total number of observations		Number consistent with contranatant behaviour	
	On bottom	In midwater	On bottom	In midwater
1	16	56	3	0
2	81	25	29	0
5	40	65	5	0
6	26	64	11	0
7	26	47	12	0
8	11	29	3	0
11	55	41	4	0
12	23	34	5	0
Totals	278	361	72	0

cloudy conditions. The moon was not visible (moonrise 0339 h) and the tide was running north (019°T). The fish was on the bottom from 2214–2236 h and briefly, for less than 2 min, at 0010 h and 0026 h. From 2240–2400 h the fish was in midwater at depths ranging from 3 to 19 m above the bottom and 2 to 24 m below the surface. When in midwater the fish was swimming through the water at speeds ranging from 21 to 78 cm s^{-1} (0·5 to 2·0 $L\ s^{-1}$).

Two sections of the track of plaice 11 were analysed, one covering sunrise and the other just before sunset. The tide was running north and the sky was overcast during both periods: the sun was not visible. In the first period (Fig. 11b) the fish moved through the water on a course of about 130°T. The fish made 4 brief excursions to the bottom at 0500 h, 0525 h, 0605 h and 0645 h. Speed through the water ranged from 9 to 90 cm s^{-1} (0·2 to 1·7 $L\ s^{-1}$). In the second

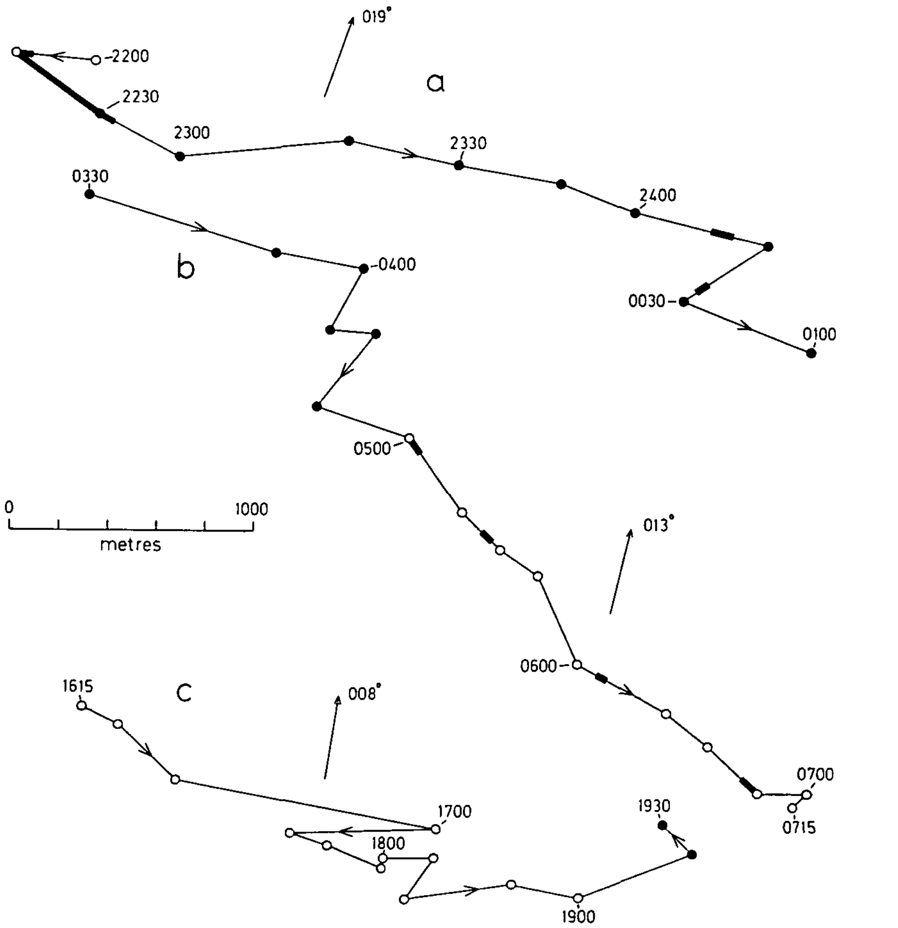

Figure 11. Progressive vector diagrams to show the movements of plaice through the water. a, plaice 8; b and c, plaice 11. Positions are shown at each ¼ h. Black circles, positions at night; clear circles, positions during the day. Thickened parts of the track indicate periods when the fish was on, or made an excursion to the bottom. The direction of the tide is shown.

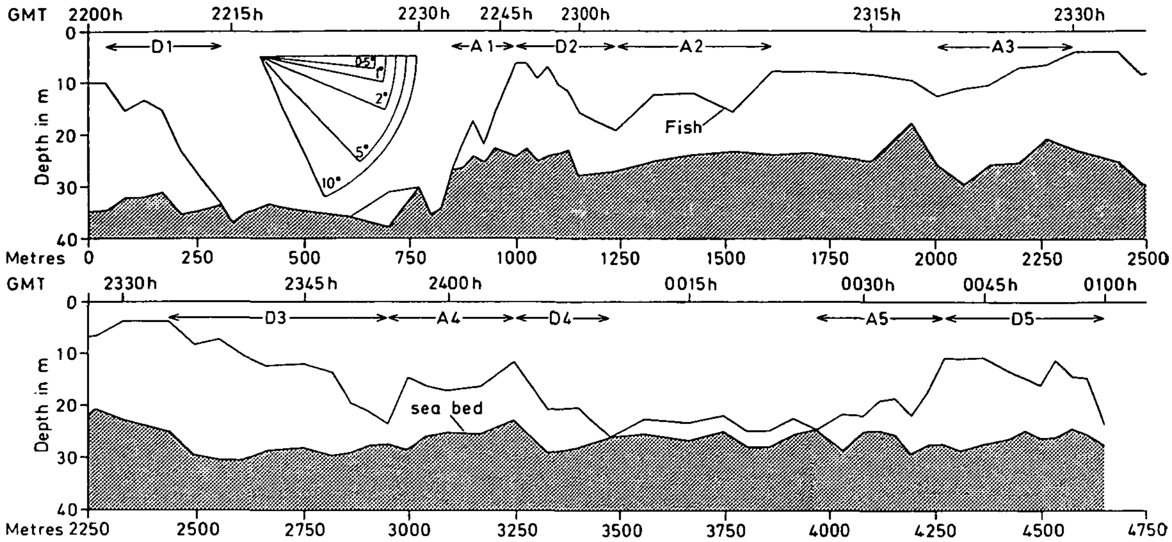

Figure 12. The trajectory of plaice 8 through the water for the period 2200 h to 0100 h (see Fig. 11a). The x-axis represents the estimated distance that the plaice moved through the water between successive depth observations which were made at 2 min intervals unless otherwise indicated. Note that the plaice approached the surface at 2250 h, 2310 h, 2330 h, 0004 h and 0042 h. The angles of ascent and descent can be determined by reference to the insert scale.

period (Fig. 11c) the overall direction through the water was approximately 095°T. The fish appeared to swim almost due west from 1700–1715 h, and then turned round to continue towards the east. Sunset was at 1930 h. The fish made no excursions to the bottom between 1615 h and 1930 h, and its speed through the water ranged from 3 to 122 cm s^{-1} (0·06 to 2·3 $L\ s^{-1}$).

Changes in depth when in midwater

Plaice changed depth in midwater and trajectories were drawn for tracks in which the speed through the water had been estimated by vector analysis. Figure 12 shows the changes in depth of plaice 8 during the period of the track covered in Figure 11a. While observations of the depth of the fish (and the sea bed) were usually made at 2 min intervals, geographical positions were fixed every ¼ h. The distance moved through the water between successive depth observations was therefore estimated on a proportional basis. While this must add some error to the estimates of the angles of descent and ascent, the results are of interest as first approximations. The angles are small[4]. Figure 12 shows that plaice 8 approached the surface on five occasions (at approximately 2250 h, 2310 h, 2330 h, 0004 h and 0042 h) at intervals of 20–35 min. Some details of the descents and ascents labelled D1 to 5 and A1 to 5 in Figure 12 are summarized in Table 17.

[4] Suggesting that speeds through the water calculated from horizontal projections (ignoring changes in depth) are not significantly underestimated.

Fish that moved less than 15 km

Three plaice (3, 9 and 10) moved less than 15 km from their release positions. Each track presents interesting features which justify a detailed description.

Tracks of individual fish

The track of plaice 3. (Track chart, Fig. 13; vertical movements, Fig. 14). Plaice 3 was released at low water slack at 0010 h on 17 June 1971 at a position 19 km ESE of Orfordness. The fish reached the bottom after 5 min and returned to midwater for ½ h before settling down on the bottom where it remained for 18 h. During this period, which extended over two southerly tides and one northerly tide, the fish moved only 3·5–4·0 km, and for some hours (see detailed insert on Fig. 13) made no detectable movement. The fish came off the bottom at 1934 h (after slack water at 1730–1830 h but before sunset at 2022 h), and stayed in midwater during the northerly tide. From 2000–2400 h the fish covered 16·2 km at a ground speed of 113 cm s^{-1}. The fish stayed in midwater during the low water slack and moved south after the tide had turned, going down to the

Table 17. Plaice 8. Movement through the water, rates of vertical movement, angles of ascent and descent, and swimming speeds for the period 2200 h–0100 h. Descents and ascents are numbered D 1–5 and A 1–5 in Figure 12

Movement	Rate of ascent or descent m min^{-1}	Speed through water cm s^{-1}	Speed through water L s^{-1}	Mean angle of ascent or descent
Descent 1	1·97	36·7	0·94	5·1°
Ascent 1	1·70	21·1	0·54	7·7°
Descent 2	0·93	29·2	0·75	3·0°
Ascent 2	1·41	77·9	2·00	1·7°
Ascent 3	0·87	53·3	1·37	1·5°
Descent 3	0·98	42·9	1·10	2·2°
Ascent 4	1·21	48·3	1·24	2·4°
Descent 4	2·40	63·3	1·62	3·6°
Ascent 5	0·98	35·9	0·92	2·6°
Descent 5	0·65	31·7	0·81	1·9°

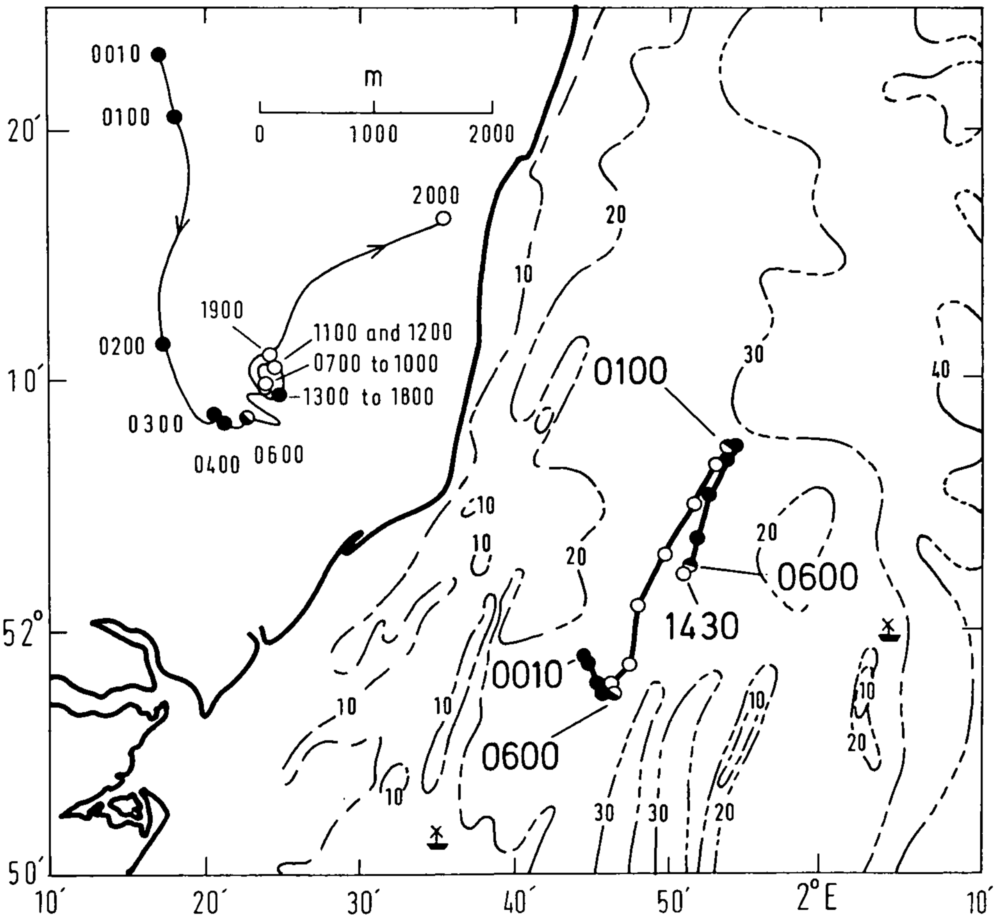

Figure 13. Track chart of plaice 3, released at 0010 h, 17 June 1971. Hourly positions of the fish are indicated and the times of slack water are given. O north-going tide, ◓ low water slack, ● south-going tide, ◒ high water slack. The insert figure shows details of the track during a northerly and a southerly tide; low water slack (at 1200 h) and high water slack (at 1800) are not specifically marked in the insert. Depth contours in metres.

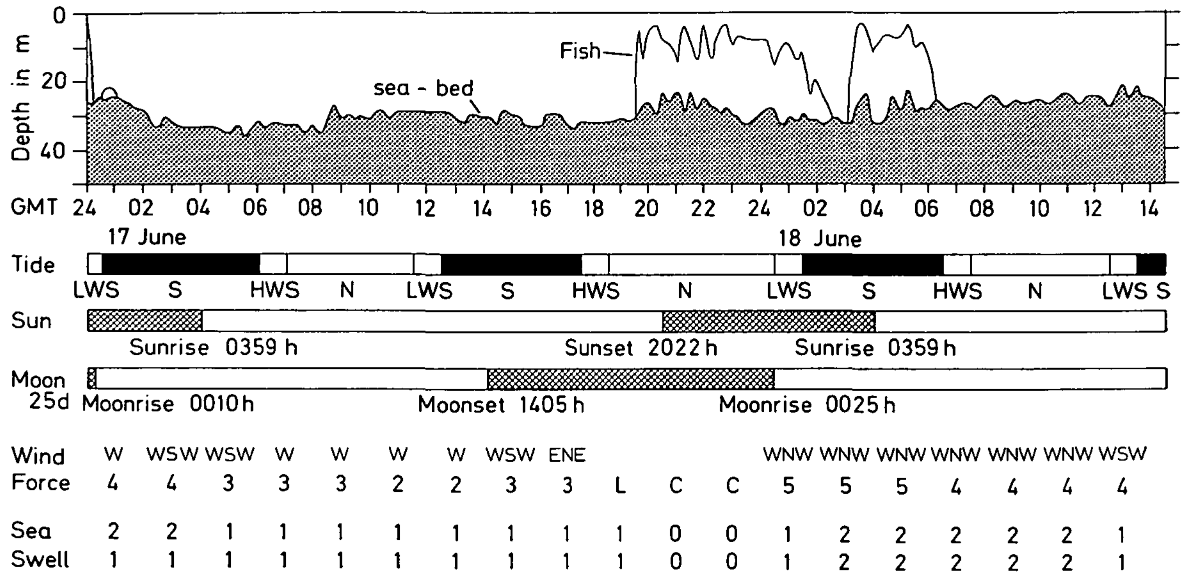

Figure 14. The depth of plaice 3 in relation to the direction of the tide and other environmental factors.

bottom at 0239 h where it stayed for 28 min. Sunrise was at 0359 h, and the sky was brightening when the fish went down to the bottom. The fish returned to midwater at 0308 h and continued to move south with the tide: from 0400–0600 h it covered 5·6 km at a ground speed of 78 cm s^{-1}. The fish went down to the bottom, without any preliminary excursion, at 0615 h (shortly before slack water at 0630–0730 h), and stayed there, moving only 50–100 m, for the rest of the track. The signal from the tag started to weaken during the morning, and although detectable, became increasingly difficult to identify against bottom reverberation and the fish was abandoned at 1430 h.

Plaice 3 left the bottom shortly before sunset and returned just over an hour before sunrise: to this extent the vertical migration could be regarded as having a diurnal (24 h) cycle. But the early return to midwater followed by a second descent at the next slack gives some indication of the semi-diurnal pattern shown by other fish. Plaice 3 was abandoned only 9 km from the position where it was released 38 h earlier.

The track of plaice 10. (Track chart, Fig. 15; vertical movements; Fig. 16). Plaice 10 was released on 13 April 1972 at a position 22 km SE × E of Orfordness and tracked for 27 h before being abandoned 12 km to the NE × N of the release position. Released at 2136 h nearly 3 h after sunset (at 1854 h) and towards the end of a southerly tide, the fish went to the bottom and stayed there until slack water (2230–2330 h). At 2310 h the fish came off the bottom into midwater where it remained, often within 4 m of the surface, until 0328 h when it returned to the bottom. The fish stayed on or just off the bottom until 0450 h (low water slack 0530–0630 h; sunrise 0508 h). The fish moved north during the northerly tide. From 2400–0328 h, when in midwater, it covered 14·8 km at an average speed of 119 cm s^{-1}, and from 0328–0450 h, when on or just off the bottom, it covered 2·7 km at an average speed of 55 cm s^{-1}.

Moving into midwater on the end of the northerly tide at 0450 h, the fish returned to the bottom at 0653 h, after the tide had turned to the south. But the fish did not settle. From 0653–0915 h its position varied from a few metres above to *just off bottom.* During this period the fish covered 7·3 km to the south at an average speed of 86 cm s^{-1}. The fish was on the bottom from 0852–0915 h and swam into midwater at 0926 h where it remained until 1925 h. During this period, which covered the second half of a southerly tide, all of a northerly tide and the first 1½ h of the following southerly tide, the fish was high in the water column and often within 4 m of the surface. The weather was good: light airs to calm, sea 1, swell 0–1. On the last 1½ h of the southerly tide (0926–1100 h) the fish went south for 5·0 km at an average speed of 89 cm s^{-1}; on the following northerly tide, from 1200–1730 h, the fish moved north for 18·7 km at an average speed of 94 cm s^{-1}; and on the next southerly tide, from 1830 h until returning to the bottom at 1952 h, the fish covered 4·4 km to the south at an average speed of 89 cm s^{-1}. For the re-

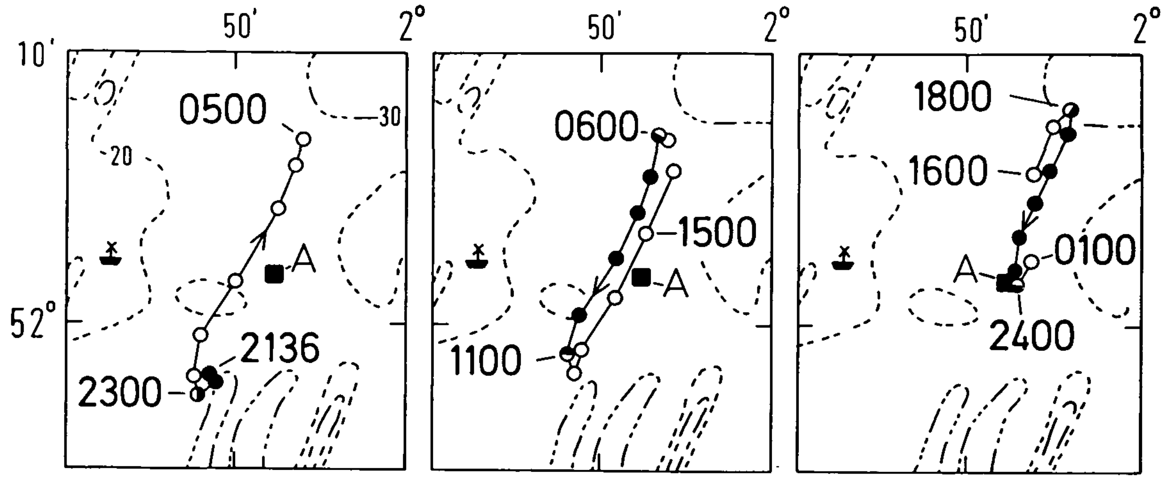

Figure 15. Track chart of plaice 10, released at 2136 h, 13 April 1972. Hourly positions of the fish are indicated and the times of slack water are given. The track has been divided into three sections to avoid superimposition. ○ north-going tide, ● south-going tide, ◑ slack water. Depth contours in metres. The position of the moored current meter (A) is indicated.

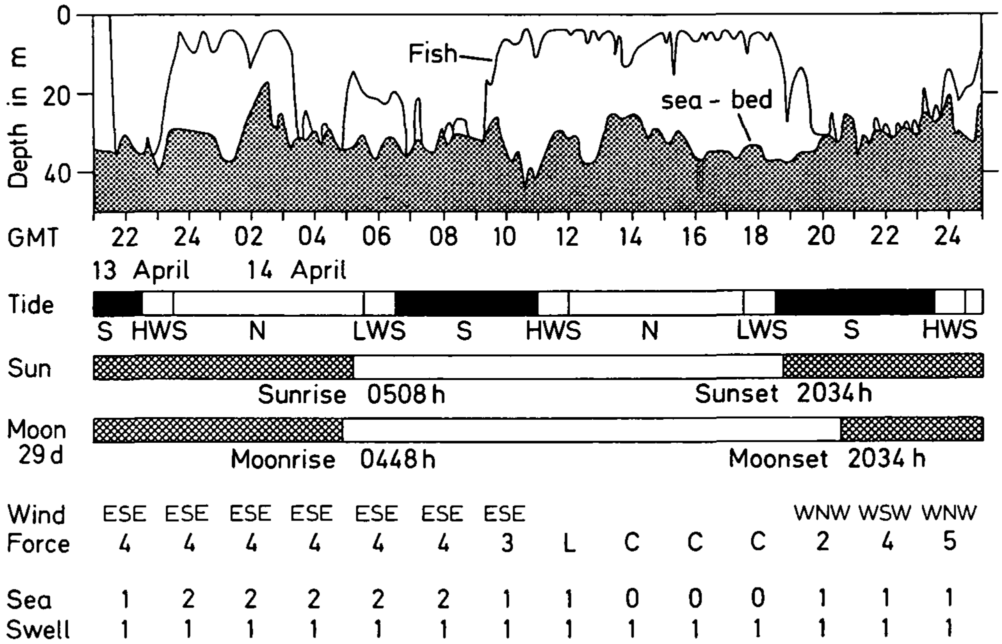

Figure 16. The depth of plaice 10 in relation to the direction of the tide and other environmental factors.

mainder of the south-going tide the fish stayed on, or just off the bottom, making eight short excursions into midwater. From 2000–2300 h the fish travelled south for 6·9 km at a speed of 64 cm s^{-1}. The fish came off the bottom at 2330 h (slack water 2330–0030 h) and staying in midwater, went north with the tide until it was abandoned at 0100 h.

Plaice 10 moved downstream irrespective of its depth in the water column and never settled in one position when on the bottom. As shown in Table 18, ground speeds were highest when the fish was in midwater (periods 1, 4, 5 and 6) and lowest when the fish was on or just off the bottom (periods 2, 3 and 7). At the end of the track the overall movement of the fish was to the NE of the release position. This was associated with reduction in ground speed during

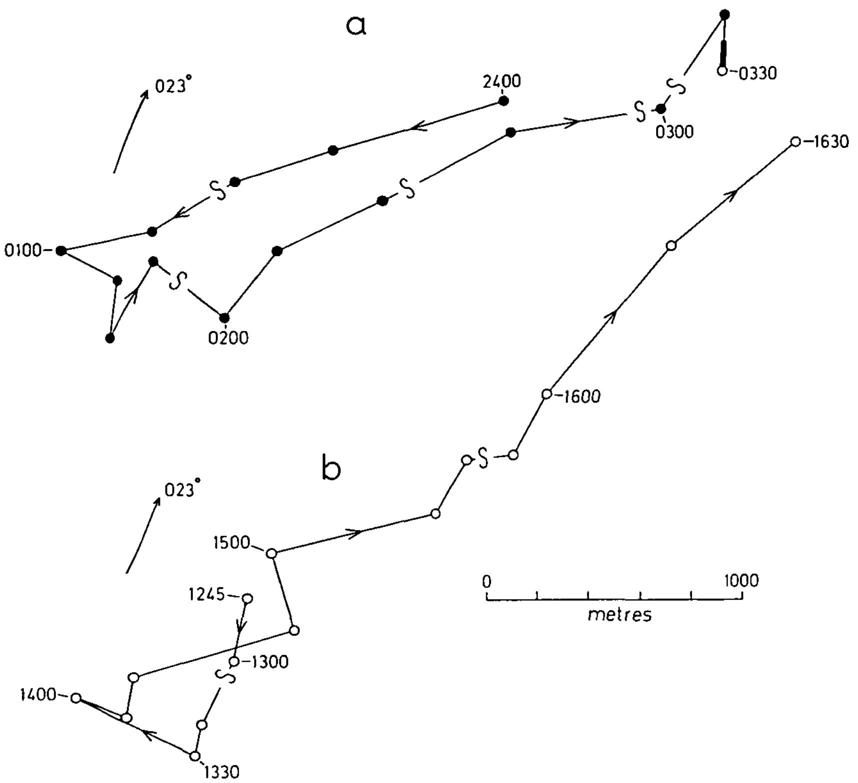

Figure. 17. Progressive vector diagrams to show the movements of plaice 10 through the water. Positions are shown at each ½ h; a, by night (black circles); b, by day (clear circles). Thickened parts of the track indicate periods when the fish made excursions to the bottom. The letter S marks periods of the track when the fish was within 4 m of the surface. The direction of the tide is shown.

the last southerly tide, the fish being near or on the bottom, and moving relatively slowly, for the last 3 h of the tide.

The movement of plaice 10 through the water was calculated by vector analysis for two periods when the fish was in midwater and the tidal speeds exceeded 70 cm s^{-1}. The tide was north-going, the first period being during the night (2400–0330 h), the second during the day (1245–1630 h). The progressive vector diagrams are shown in Figures 17a and b which show that the fish maintained a more or less steady course through the water for periods up to

Table 18. Plaice 10. Relation between tidal direction, position in the water column, distance and direction moved and speed over ground

Observation period	Time GMT	Direction of tide	Position and movement of fish: Position in water column	Distance moved in km	Course over ground in °True	Speed over ground cm s^{-1}
1	2400–0328	north	in midwater	14·8	025°	119
2	0328–0450	north	near or on bottom	2·7	018°	55
3	0653–0915	south	near or on bottom	7·3	202°	86
4	0926–1100	south	in midwater	5·0	208°	89
5	1200–1730	north	in midwater	18·7	025°	94
6	1830–1952	south	in midwater	4·4	201°	89
7	2000–2300	south	near or on bottom	6·9	195°	64

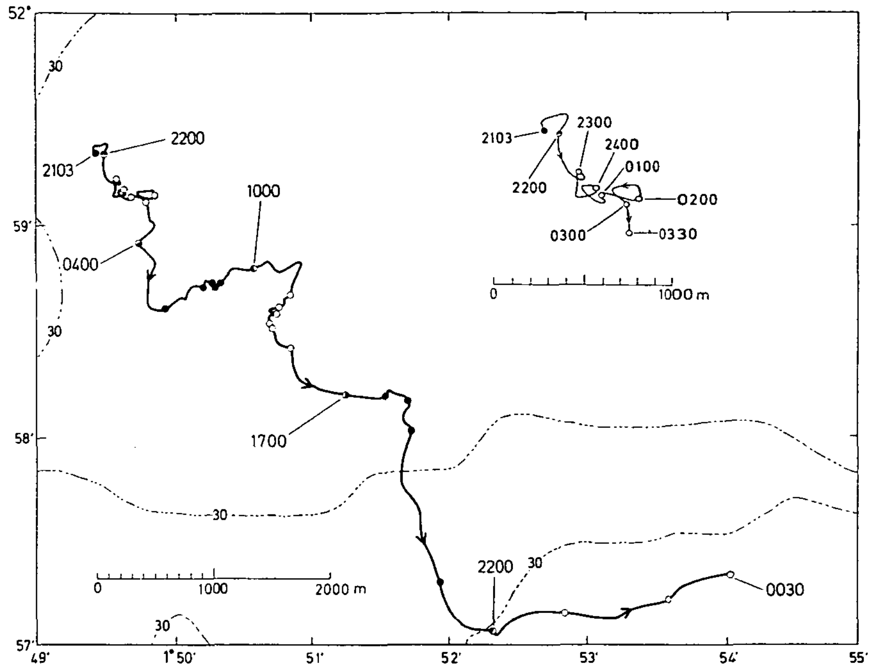

Figure 18. Track chart of plaice 9 released at 2103 h, 11 April 1972. Hourly positions of the fish are indicated and the times of slack water are given. o north-going tide, ● south-going tide, slack water. The insert figure shows the 3 anti-clockwise circles completed during the first part of the track. Depth contours in metres (from British Admiralty Chart L(D5) 2052).

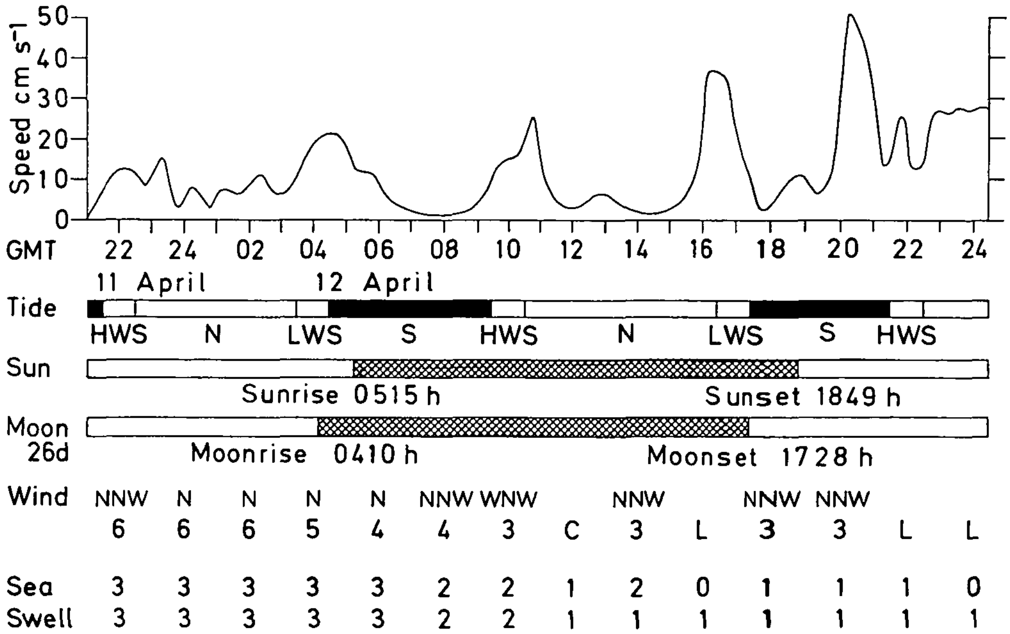

Figure 19. The speed of plaice 9 over the ground (as determined from the distance travelled between 30 min fixes) in relation to tide and other environmental factors.

1½ h. Both tracks showed sudden changes of course and the speed through the water ranged from 14 to 87 cm s^{-1} (0·3 to 2·0 L s^{-1}).

The track of plaice 9. (Track chart, Fig. 18; activity, Fig. 19). Plaice 9 was released at 2103 h on 11 April 1972 at a position 19 km SE × E of Orfordness, 30 min before low water slack. Six minutes after release the fish reached the bottom at 29 m and did not move into midwater during the 27 h track which ended at 0030 h, 13 April. The fish was then abandoned 6·5 km ESE of the release position. While the track chart shows that the overall movement of the fish was to the southeast, there were some striking changes in speed and direction.

Figure 19 shows the fish's speed over the ground, calculated from the distance between 30 min fixes. Three peaks in swimming speed over the ground (0400–0500 h, 1000–1100 h and 1600–1700 h) close to the slackwater periods (0330–0430 h, 0930–1030 and 1630–1730 h) suggest a quarter-diurnal rhythm of activity.

Figure 18 shows the track falls into 4 sections, separated by three marked changes of course of approximately 90° as summarized in Table 19. The course changes at 0500 h, 1045 h and 2200 h were close to slack water (0330–0430 h, 0930–1030 h and 2130–2230 h). But there was no marked change of course associated with slack water at 1630–1730 h.

The first section of the track was twisted and as shown in the insert on Figure 18, the fish completed three anti-clockwise circles over the ground with diameters of approximately 50, 100 and 200 m respectively.

Data relating the last 5½ h of the track, from 1900–0030 h, are shown in Figure 20. Moonset was at 1728 h (age 27 d) and sunset at 1849 h. The wind was NNW force 3, decreasing to light airs; sea state 1, decreasing to 0, swell 1; the sky was overcast. The fish's speed over the ground was calculated from the distance between 15 min fixes, and at 2000 h there was a marked increase in speed from 8–15 cm s^{-1} to over 45 cm s^{-1}. There did not appear to be any obvious environmental factor associated with the change of speed: while the fish was moving into deeper water the increase in speed occurred before an appreciable increase in depth. Between 2100 h and 2200 h the fish moved into and out of a relatively steep-sided hole with a maximum depth of 60 m[5]. The fish slowed down to speeds of 8 and 6 cm s^{-1} when going down and coming up the steepest parts of the hole, the change in depth of the fish suggesting seabed gradients of 1 in 8·6 and 1 in 3·9 respectively[6]. After leaving the hole, the fish changed course between 2215 and 2230 h and from 2230–2235 h was recorded as *just off bottom* (see p. 60) for the first time during the track. Slack water was within the hour 2130–2230 h.

The sector scanner display showed that the fish moved into and out of the hole on a course parallel to the crests of sandwaves which were conspicuous and regular features of the bottom in this area. The crests of the sandwaves were asymmetric, the steep slopes facing ENE: the tide was running to the north when these observations were made. Movement over the ground followed a consistent pattern, the fish swimming along the hollows between two sandwaves for 200–300 m turning left (north) to cross one or two crests, and then turning to its right (south) to start a second leg between another two sandwaves[7]. Thus the approximately 90° change of course made by the fish shortly after 2200 h was associated with movement normal to rather than parallel to the sandwaves (see Fig. 18). The fish was still keeping to the new course, and the new alignment to the sandwaves, when the track was ended at 0030 h on 13 April. While this was the first occasion on which the movements of a fish were clearly related to features of bottom topography a study of films and notes made during earlier tracks showed that it was not unique: similar behaviour was noticed during the track of plaice 1 and plaice 5.

Table 19. The track of plaice 9, 2103–0030 h, 11–13 April 1972. For track chart see Figure 18

Observation period	Time GMT	Overall course over the ground °True
1	2103–0500	155°
2	0500–1045	070°
3	1045–2200	153°
4	2200–0030	076°

[5] This hole, centred at about 50°57·1'N 01°52·0'E, is not shown on British Admiralty metric chart L (D5) 2052 (1974) but its presence is recorded by a 28 fm sounding on an earlier chart L (D5) 1504 (1965). The hole was surveyed again in December, 1976 (RV "Corella" 15/76): it lies in a depression associated with one of the tunnel valleys described by D'Olier (1975).

[6] We have some confidence in the depth measurements from which these gradients were calculated. There was usually a close agreement between the depth of the sea bed as recorded by RV "Clione"s navigational echo sounder and the depth of the fish on the bottom as calculated from the sector scanner when used in vertical mode. On a level bottom (stations 310–328 in Fig. 20) differences did not exceed ± 1 m.

[7] Long sequences of this swimming behaviour were filmed but the reel was irreparably damaged by a faulty camera.

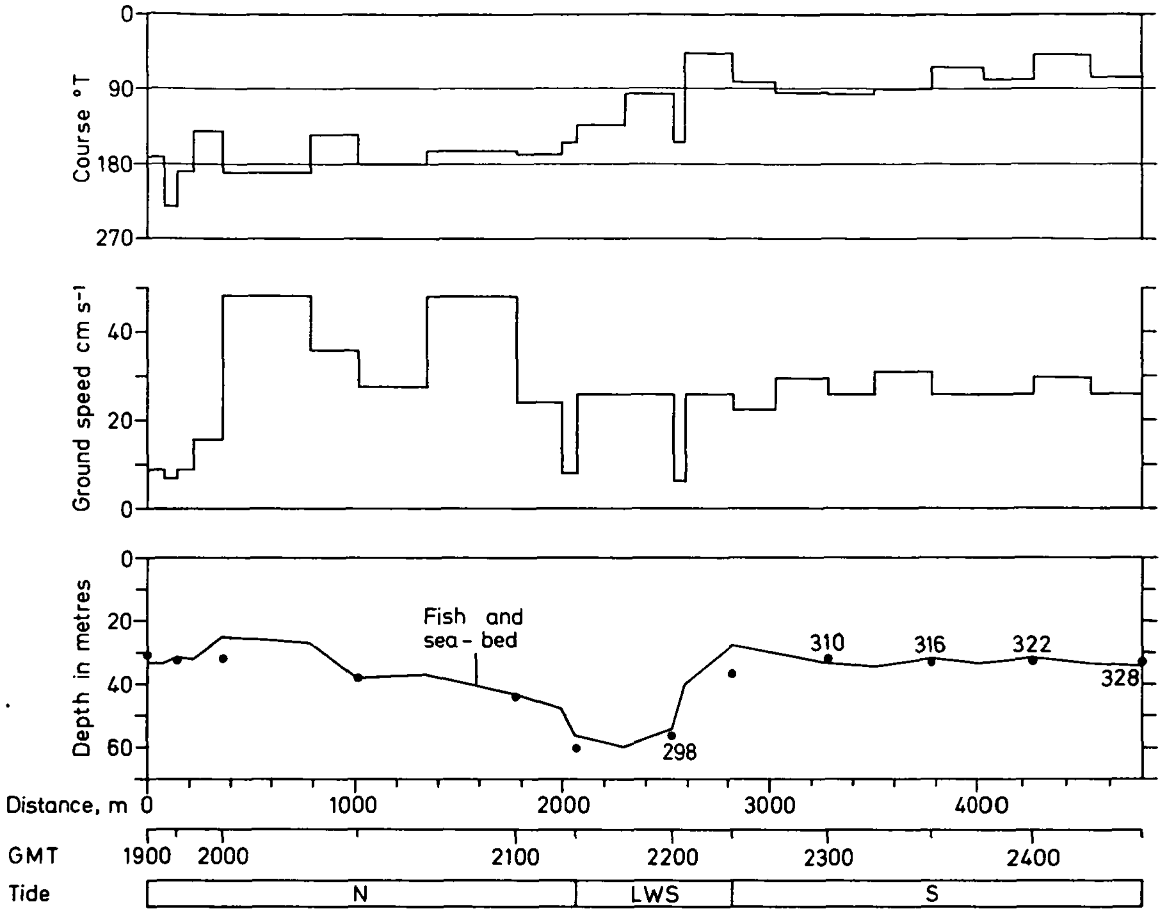

Figure 20. The direction and speed over the ground of plaice 9 as determined from 15 min fixes during the last part of the track. The depth of the fish (and thus the sea bed) as calculated from the sector scanner display is also shown. The black circles show the depth recorded by RV "Clione"s echo sounder; note the good agreement between the two sets of observations when the bottom was level (stations 310–328). There is a discrepancy between the depths recorded at station 298 (2200 h) and the position of the 30 m depth contour on Figure 18.

Discussion

Observations made at sea on plaice previously held in the laboratory are open to the criticism that however fit the fish may appear as judged by colour, activity, appetite or weight, their behaviour may be abnormal. Unfortunately the very nature of this work – and that on the efficiency of the Granton trawl (Harden Jones et al, 1977) – precludes the use of controls to settle the point: a direct comparison cannot be made between the behaviour of a wild plaice and that of a fish which has been caught, held in the laboratory, fitted with an acoustic tag and released in the open sea. Some of the plaice abandoned in the tracking and gear studies have been caught by fishermen and returned to the laboratory: half of these fish still carried the acoustic tag[8]. While these fish were in good condition and were returned from the English Channel and the southern and middle North Sea in positions consistent with normal behaviour, the returns do not give any information about their behaviour during the first 48 h after release. Confidence in the validity of the sector scanner observations would be established if predictions made from the behaviour of individual tagged fish could be confirmed by independent studies on the wild population. This has been possible in connection with the

[8] From July 1970 to November 1976, 97 plaice fitted with acoustic transponding tags were left in the sea. By April 1977, 44 fish had been recaptured and in 22 cases the acoustic tag was returned.

vertical distribution of migrating plaice (Harden Jones, Greer Walker and Arnold, in press), and we have concluded that the behaviour patterns observed using the transponding tag-sector scanner technique are probably similar to those of wild plaice.

There is no evidence to suggest that the fish were disturbed by noise from RV "Clione" (p. 61). A similar lack of response to engine noise was observed in the Granton trawl work (Harden Jones et al, 1977, p. 50). The depth at which the plaice swam below the surface did not appear to be affected by weather up to sea state 3. Only 10 depth observations (made at 15 min intervals) are available at sea states 4 and 5 and in each instance the fish was 20 m or more below the surface. Bad weather (wind NNE Force 7, sea 4, swell 4) during the track of plaice 2 (see Fig. 7) was associated with the fish, rather exceptionally, staying on the bottom during a northerly tide. Taken together these observations are consistent with the suggestion that the depth at which the fish swims below the surface could be affected by the weather.

Many of the tracks gave new information on the movements and behaviour of plaice in the sea but discussion will be limited to a few points.

There was no obvious explanation to account for the difference in behaviour between fish whose overall movement was north or south, or stayed in midwater or on the bottom. Differences in behaviour could not be related to the grounds on which the fish were caught as they were at one stage held in the same reception tank and allowed to mix.

The behaviour of plaice 9 in relation to sandwaves (see p. 82) showed that the direction of movement on the bottom could be influenced by topography. Some fish went round in circles (plaice 3, Fig. 13; plaice 7, Fig. 2; plaice 9, Fig. 18) which had diameters up to 200–350 m. We think that these movements are probably real and do not reflect errors in the research vessel's navigational equipment. The circular movements of plaice 9 were observed in an area which appeared to be free of sandwaves.

When plaice were on the bottom, the signal from the transponding tag was often difficult to detect. Manoeuvring the research vessel did not always lead to any improvement which suggested that both fish and tag were partially buried. Sudden and sharp increases in signal strength from such tags suggested that the fish was making small movements in the bottom without a change of position.

When in midwater plaice changed depth at angles which are less than those considered by Weihs (1973) for energy saving by a swim-and-glide pattern of locomotion. These observations suggest that plaice may not save energy in this way. This would not be surprising as the potential saving is probably small when compared with that likely to accrue from selective tidal stream transport itself (see below and Weihs, 1978), which might, in an evolutionary sense, overshadow lesser economies. It would be interesting to study an oceanic species, such as bluefin tuna, from this point of view. Our results do not tell us whether plaice swim actively or glide when descending: heart rate telemetry and monitoring fin movements might help to elucidate this problem.

The most consistent, and the most interesting, behaviour pattern observed in the tracking work is that which we have called selective tidal stream transport: fish leave the bottom at slack water to move downstream in midwater on one tide, and return to the bottom at the next slack, with little, or no significant movement on the opposing tide. Plaice behave in this way both by day and by night. The transport system is similar to that shown by Creutzberg (1961) to account for the inshore migration of elvers (*Anguilla anguilla*) and by Hughes (1969) for the inshore and offshore migrations of the shrimp (*Penaeus duorarum*). De Veen (1967) suggested that soles used tidal transport during their spawning migration, the fish joining the appropriate tide only during the night. If selective tidal stream transport was maintained over several tidal cycles in the southern North Sea, the behaviour pattern would allow plaice to move for substantial distances at average ground speeds similar to those deduced for migrants from conventional tagging experiments (Harden Jones et al, in press) and as shown by Weihs (1978) in a paper in this Journal, could also lead to a reduction in the energy cost of migration.

Plaice spawn in the Southern Bight of the North Sea from December to March, peak egg production being in January, usually within the area bounded by latitudes 51°30′–52°N and longitudes 2°–3°E, where the Hinder Ground (51°45′N 2°30′E) is a convenient place to mark the spawning centre. Earlier tagging experiments (reviewed by Harden Jones, 1968, p. 171) have shown that maturing plaice leave the middle North Sea to spawn in this area, moving south within the longitudes 2°E and 3°E, and returning north as spent fish by the same route. If the plaice used selective tidal stream transport while on migration, mature fish should be in midwater on south-going tides and spent fish in midwater on northerly tides. Midwater fishing with an Engel trawl (for a preliminary account of this work see Harden Jones et al, in press) has confirmed this prediction and these results are consistent with the hypothesis that fish use tidal stream transport for migration in shelf areas where tides are strong.

The hypothesis raises problems in connection with timing and discrimination which can be considered under three headings. Firstly, a fish must be locked on, or entrained, to the appropriate tide which will take it from the initial position to the final destination. Secondly there must be a mechanism to maintain the semi-diurnal pattern of vertical movement so that the fish joins the correct tide when migrating: thirdly, the fish must leave the transport system when the spawning area, or ground, is reached. If a similar transport mechanism is used by the spent fish, similar problems will arise on the return journey.

While the results described in this paper do not help us to understand how a fish joins the appropriate tide[9] or how the spawning area is recognised, they give some indication of the behavioural mechanisms involved in maintaining the link with the transporting tide when the migrants are on passage. The fact that ascents are more closely related to slack water than descents, and that descents are usually preceded by excursions to the bottom, suggests that both a rheotropic response, mediated through sight of or contact with the bottom, and a semi-diurnal rhythm of activity entrained to the tidal cycle, are involved in the synchronising mechanism.[10] It will be recalled that plaice 9, which remained on the bottom, showed an increase in activity at slack water: other fish (see p. 73) also became more active at slack water before moving into midwater.

Plaice gained ground against the tide when on the bottom but not when in midwater. But the results of the vector analyses described on p. 75 suggest that plaice may maintain a consistent heading when in midwater. Plaice 7 appeared to swim downstream on a northerly tide, while plaice 8, 10 and 11 maintained a steady course through the water for up to $1\frac{1}{2}$ h or more. Even when the likely sources of error are taken into consideration, these results appear to be reasonably convincing and one of the tracks of plaice 11 recalls the easterly headings of soles reported by de Veen (1967). We do not have any useful suggestions to make as to the sensory mechanisms on which this behaviour could be based: further observations are required. Progress could be made if the compass heading of the fish and other relevant information could be returned "on line" to the research vessel by a transponding telemetering acoustic tag. Such a tag is being developed at the Fisheries Laboratory, Lowestoft. To make the best use of the new tag the position fixing of the research vessel would have to be improved by an order of magnitude to match the resolution of the sector scanner display and the work would need to be supported by the tactical deployment of current meter arrays as suggested by Ramster and Medler (1978) in this Journal.

[9] Selective tidal stream transport was shown by two plaice fitted with small but powerful permanent ring magnets (Mullard FD 364, Magnadur 1, pole field intensity 500–600 gauss) which suggests that clues involving the earth's magnetic field are unlikely to be involved.

[10] Rheotropic responses of plaice have been described by Arnold (1969) and semi-diurnal rhythms by Gibson (1976).

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