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Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea

G. P. Arnold, M. Greer Walker, L. S. Emerson, and B. H. Holford

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Twenty-four cod fitted with 300 kHz transponding acoustic tags were tracked by sector- scanning sonar in the southern North Sea for periods up to 52 h and over distances up to 72 km. Three fish were released at the surface; the others were released on the sea bed at depths of 24 to 73 m after a period of enforced pressure adaptation in a small cage. Tidal currents, which were measured with moored current meters during five tracks, strongly influenced all movements. The three fish released at the surface were transported to and fro over the ground by successive tides, as were five fish that moved net distances of 15 to 20 km off-shore across the tidal stream axis when released close to the East Anglian coast. Three cod released east of the Norfolk Banks moved net distances of 40 to 70 km to the north by selective tidal stream transport. Another released north of the Banks swam to the east along the tidal stream axis. Most of these cod turned to head against the prevailing tide when they went to the seabed and one that showed tidal stream transport in an area of moderate tidal currents made ground against the opposing tide when it was on the bottom. Several fish maintained a heading in midwater for a number of hours and one deviated by no more than $\pm 45°$ from its mean heading during an 8-h period. Three fish made slow sweeping turns in midwater to adopt a downtide heading after previously swimming across the tide. Average swimming speeds in midwater were 0.3–0.9 L s^{-1} and similar speeds were estimated for fish in the bottom boundary layer: ground speeds, which reflected the speed of the tidal current, were proportionately greater than through-water speeds. Several fish made pronounced vertical movements to or from the seabed at or near sunrise or sunset and one fish showed a diel pattern of vertical migration. The results are discussed in relation to the sensory cues and clues that might be used for orientation and migration, swimming performance, and the role of selective tidal stream transport in the spawning migrations of cod in the southern North Sea.

Key words: cod, migration, selective tidal stream transport, swimming speed, orientation, sensory cues and clues.

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G. P. Arnold, M. Greer Walker, L. S. Emerson, and B. H. Holford: Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Fisheries Laboratory, Lowestoft, Suffolk NR33 0HT, England.

Introduction

Selective tidal stream transport (Arnold, 1974, 1981; Greer Walker *et al.*, 1978) is an important feature of the life history of the plaice (*Pleuronectes platessa* L.) in the Southern Bight of the North Sea from metamorphosis onwards (Creutzberg *et al.*, 1978; Greer Walker *et al.*, 1978; de Veen, 1978; Harden Jones *et al.*, 1979; Rijnsdorp *et al.*, 1985). The behaviour is also observed in soles (*Solea solea*) (de Veen, 1967, 1978; Greer Walker *et al.*, 1980; Greer Walker and Emerson, 1990), flounders (*Platichthys flesus*) (de Veen, 1978), dogfish (*Scyliorhinus canicula*) (Greer Walker *et al.*, 1980), and both the American eel (*Anguilla rostrata*) (McCleave and Kleckner, 1982) and the European eel (*A. anguilla*) (Creutzberg, 1961; Arnold, 1981; McCleave and Kleckner, 1985). Theoretically, the mechanism can provide both a transport and a guidance system for migrating fish over much of the European continental shelf (Arnold and Cook, 1984), and several questions therefore arise. Does tidal stream transport occur in roundfish as well as flatfish and is it therefore a general feature of the migrations of demersal fish on the shelf? Is the behaviour limited to areas of fast tidal streams or does it occur elsewhere where the tidal currents can provide a source of directional information, even though

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they are not sufficiently fast for migrating fish to gain an energetic advantage?

This paper describes the results of a series of tracking experiments with free-ranging cod (*Gadus morhua* L.) in the southern North Sea between 1971 and 1979, which provide partial answers to these questions. The experiments were conducted with fish caught off Lowestoft and assumed to belong to the cod population that migrates annually between summer feeding grounds in the central North Sea and winter spawning grounds in the Southern Bight and eastern English Channel (Daan, 1978). Fish of this population occur along the East Anglian coast in autumn and winter (Bedford, 1966). The aims of the work were to follow the movements of free-ranging fish during the period of the post-spawning migration and investigate their behaviour and orientation in relation to that of the tidal streams. Individual fish were released at various places along the likely migration route at what were thought – from an inspection of conventional tag returns (Bedford, 1966) – to be appropriate times. Wherever possible, the heading of the fish and its speed through the water were deduced from measurements of tidal stream vectors made with recording current meters. The vertical movements of the fish have been described in a previous paper (Arnold and Greer Walker, 1992), where they are analysed in relation to the hydrostatic function of the swimbladder; some figures are repeated here with additional information. Full details of all tracks are published by Buckley (in press).

Material and methods

The fish

Cod were caught by rod-and-line or long-line close to Lowestoft in an area of shallow water, where the depth did not exceed 8 m. They were brought slowly to the surface. There was no evidence of the swimbladder being inverted through the mouth, and the maximum pressure reduction of 44% was such that there should have been no risk of rupture, or irreversible damage, to the swimbladder wall (Tytler and Blaxter, 1973). The fish were caught during winter when post-spawning cod feeding along the East Anglian coast are regularly taken by beach anglers fishing in the inter-tidal zone. Fish in good condition were kept in a large holding tank (4.8 × 3.6 × 0.9 m deep) with a constant flow-through of clean sea water at 10°C for periods up to several months. They were fed to satiation twice weekly on a diet of lugworm (*Arenicola marina*) and chopped fish. Immediately prior to a cruise the fish were placed on board ship in galvanized iron deck tanks (1.85 × 0.9 × 0.7 m deep) with a copious supply (30 l min^{-1}) of clean seawater. Before release the length of the fish was recorded and a spaghetti tag inserted through the dorsal muscles at each end of the first dorsal fin. During tagging each fish was blindfolded with wet paper towels and the gills irrigated with seawater. With the exception of cod 3, no anaesthetics were used and the fish usually remained quiescent during the tagging process. Cod 3 was anaesthetized in MS 222 at a dilution of 1:15 000.

The equipment and tracking procedures

The transponding acoustic tag (0.8 cm diameter, 5.1 cm length; Mitson and Storeton-West, 1971) was tied between the two spaghetti tags using braided nylon thread with the transducer pointing towards the tail of the fish. The acoustic tag returned a 3-ms pulse when insonified at 300 kHz by the sector-scanning sonar (Voglis and Cook, 1966) installed aboard RV "Clione" (Mitson and Cook, 1971). The tag weighed only 3–4 g in seawater and was unlikely to have decreased the swimming speed of the fish significantly (Arnold and Holford, 1978). The recovery in good condition of cod 3, which was caught by an angler off the beach between Great Yarmouth and Lowestoft (Fig. 1) 10 days after the end of the track (Table 1), suggests that the tag had few adverse affects on the fish.

During each track the fish was kept under constant surveillance and its position recorded every 15 min. Range from the ship was estimated directly from the sonar screen to the nearest 5 m and bearing or depth to the nearest 1°. The depth of the fish was recorded more frequently during the midwater portions of some tracks. The position of the ship was determined every 15 min by reference to the Decca Navigator system. Variable Decca errors ranged from ± 80 to ± 200 m by day and ± 370 to ± 1400 m by night, depending on chain, location, and season (Anon., 1973). The effect of the larger night-time errors can be seen in Figures 9a and 9c. The main portions of the tracks of cod 4–9 ran roughly normal to the major axis (75–255°) of the diamond of error formed by the intersecting red and green lanes of chain 5B south of Smiths Knoll. For these fish the day-time and night-time errors along the line of the track were ± 50 m and ± 140 m, respectively, which compare with typical distances over the ground between successive 15-min fixes of 100–200 m at slack water and 1000–1500 m during midtide.

The release cage

Cod 1, 2, and 3, which were adapted to atmospheric pressure, were released at the surface. The other 21 fish were released on the seabed after a period of confinement (Table 1) in a small cage, during which they had the opportunity to adapt, or partially adapt, to ambient pressure. The cage (1.2 × 0.9 × 0.5 m high) was constructed of light steel angle lined with knotless netting. The base consisted of a perforated and hinged door,

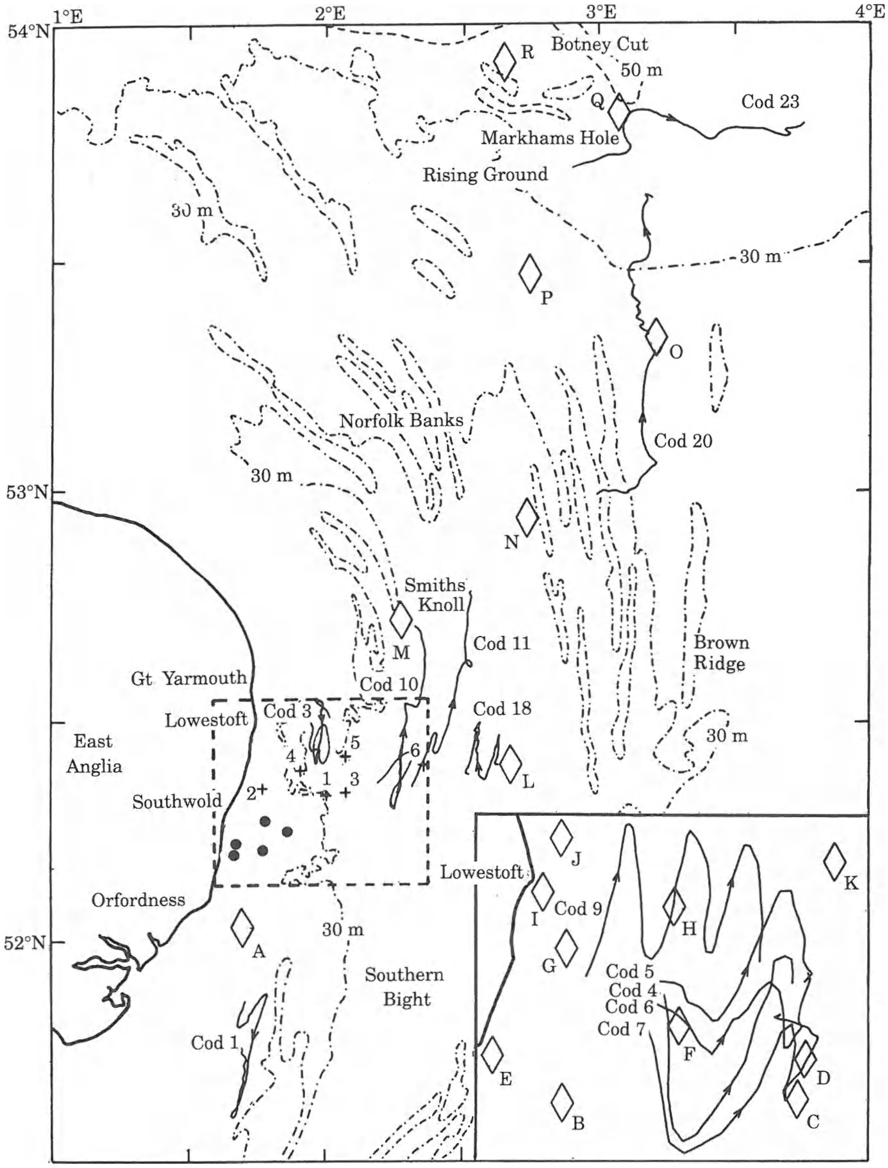

Figure 1. A chart of the southern North Sea showing the positions of the tracks in relation to the main topographical features. Positions of current meter rigs (+), near-bed current measurements (●), and selected British Admiralty tidal stations (◇) are also shown. Coastline and isobaths from British Admiralty Chart 2182A. In this and other geographical figures 1′ of latitude is equal to 1 nautical mile (1853 m). The insert shows the positions of the tracks of cod 4–9 in the area off Lowestoft indicated by the dashed box in the main figure. Cod 2 was tracked in the same location as cod 3.

which swung open as the cage was raised from the seabed (Shreeve *et al.*, submitted).

The working area

The cod were released and tracked in the area between latitudes 51°40′ and 54°N, longitudes 1°40′ and 3°45′E (Fig. 1). About half the fish were released off the East Anglian coast in shallow turbid water (depth 20–25 m), where there are fast tidal streams and the bottom deposits are mainly medium sand (0.25–0.5 mm grain diameter) with local beds of gravel (Harrison and Ardus, 1990). Sand waves (λ=2–3 m) lie normal to the axis of the tidal streams in some places and there are occasional patches of larger sand waves. Several cod were released to the east of Smiths Knoll in the deeper water (30–50 m), which extends from the central Southern Bight to approximately 53°15′N. Two fish were released near the

Table 1. Details of cod fitted with acoustic transponding tags and released in the southern North Sea during the period June 1971–May 1979. Cod 1–3 were adapted to atmospheric pressure and were released at the surface. The remainder were released at the seabed after a period of enforced pressure adaptation in a small cage (Shreeve *et al.*, submitted). Positions are given in degrees and decimal minutes. HWS and LWS indicate high- and low-water local slack tide, respectively.

Release data						State of tide					Movement over ground		
Cod no.	Length (cm)	Date	Time (GMT)	Depth (m)	Adaptation time (h)	North- or south-going stream	Spring (Sp) or neap (Np)	Release position	Final position	Track duration (h)	Direction (°T)	Net distance (km)	Overall distance (km)
(a) Cod released at the surface													
1	53	12 Jun 1971	1213	37	—	S	Sp	51°50.4'N 01°46.0'E	51°41.0'N 01°45.7'E	50.5	181	17.3	77.5
2	50	20 Nov 1972	1002	24	—	S	Np–Sp	52°17.3'N 01°55.9'E	52°24.2'N 02°01.6'E	52	027	14.3	162.1
3	72	27 Nov 1972	1926	30	—	N	Sp–Np	52°29.3'N 02°01.7'E	52°30.7'N 01°58.6'E	38.5	306	4.2	112.0
(b) Cod released off the East Anglian coast													
4	—	21 Apr 1974	1800	32	2.0	S	Np–Sp	52°21.8'N 01°58.7'E	52°22.6'N 02°11.0'E	14.5	084	14.1	45.2
5	—	25 Apr 1974	0845	36	20.0	S	Sp	52°22.6'N 01°59.4'E	52°22.7'N 02°12.7'E	16.8	090	15.0	36.2
6	50	26 Apr 1974	2012	30	11.7	LWS	Sp	52°21.4'N 01°57.8'E	52°23.1'N 02°13.0'E	25.3	080	17.5	39.5
7	60	28 Apr 1974	1115	32	12.0	S	Sp–Np	52°20.1'N 01°57.1'E	52°21.6'N 02°10.3'E	29.8	081	16.3	65.8
8	69	19 Apr 1975	1015	24	24.0	N	Np	52°22.2'N 01°50.2'N	— —	2.0	—	—	—
9	69	21 Apr 1975	0700	22	37.2	HWS	Np	52°23.2'N 01°50.1'E	52°23.8'N 02°08.1'E	36.8	087	20.3	93.1
18	62	27 May 1977	0821	47	61.3	N	Np	52°25.1'N 02°37.1'E	52°24.2'N 02°31.4'E	22.6	254	6.7	45.7
19	71	28 May 1977	2230	45	100.1	N	Np	52°25.3'N 02°34.1'E	52°24.2'N 02°34.5'E	19.5	004	6.7	18.9

Table 1. *Continued.*

Release data						State of tide				Track	Movement over ground		
Cod no.	Length (cm)	Date	Time (GMT)	Depth (m)	Adaptation time (h)	North- or south-going stream	Spring (Sp) or neap (Np)	Release position	Final position	duration (h)	Direction (°T)	Net distance (km)	Overall distance (km)
(c) Cod released south and east of the Norfolk Banks													
10	63	24 Apr 1975	1300	40	28.4	N	Sp	52°22.8′N 02°12.7′E	52°45.6′N 02°15.7′E	43.2	005	42.5	113.9
11	66	27 Apr 1975	1530	44	22.3	N	Sp	52°22.0′N 02°19.8′E	52°47.0′N 02°32.3′E	27.0	017	48.4	69.8
12	76	13 May 1976	1537	44	49.5	N	Np–Sp	52°57.1′N 02°32.3′E	— —	3.1	—	—	—
13	68	29 Mar 1977	0905	35	73.1	S	Np	53°04.8′N 02°46.4′E	— —	0.5	—	—	—
14	68	29 Mar 1977	1046	36	76.0	S	Np	53°02.7′N 02°44.0.′E	53°03.4′N 02°48.7′E	28.7	077	5.3	56.4
15	73	31 Mar 1977	0906	34	47.0	S	Np	53°04.7′N 02°46.6′E	53°13.2′N 02°49.1′E	6.5	010	15.9	19.8
16	59	1 Apr 1977	1745	30	45.6	S	Np	53°23.9′N 02°48.1′E	53°22.1′N 02°50.8′E	1.7	138	4.6	5.6
17	64	3 Apr 1977	1215	31	88.7	N	Np–Sp	53°24.3′N 02°44.9′E	53°33.7′N 02°53.1′E	23.3	027	19.7	66.0
20	69	30 May 1977	1915	24	53.0	S	Np–Sp	53°00.1′N 03°00.8′E	53°38.4′N 03°11.8′E	51.0	010	72.1	116.4
(d) Cod released north of the Norfolk Banks													
21	68	3 Jun 1977	1852	25	149.7	S	Sp	52°56.2′N 02°57.0′E	— —	4.1	—	—	—
22	76	18 Apr 1978	1156	40	76.9	N	Sp	53°39.2′N 02°55.3′E	53°39.3′N 02°55.3′E	0.8	335	0.2	—
23	76	21 Apr 1978	1530	40	71.8	N	Np–Sp	53°41.4′N 02°57.6′E	53°46.4′N 03°46.7′E	37.6	080	54.7	78.8
24	63	30 May 1979	0851	73	136.0	S	Sp	53°49.9′N 02°39.6′E	53°50.4′N 02°38.4′E	6.1	307	1.7	2.4

Rising Ground: here the bottom deposits are fine sand and soft mud, with sand and shingle in the shallower parts. The last fish was released in deeper water (40–80 m) near Markhams Hole (Fig. 1).

Tidal stream speeds and directions

Times of slack water and speeds and directions of tidal streams were estimated from data provided on British Admiralty charts. During the tracks of cod 4–9 one or two recording current meter rigs (Baxter and Bedwell, 1972), programmed to record the speed and direction of the water current every 10 min, were moored in the intended tracking area (Fig. 1). Three more rigs were deployed in the same area in April 1980 to assess the variation in the tidal streams with distance from the coast. Rigs 2 and 4 had single current meters at heights of 6 and 17 m above the seabed in water depths (MLWS) of 22 and 27 m, respectively. The other four rigs supported one current meter near the seabed (height above bottom 6–8 m) and one near the surface at a depth (mean spring tides) between 5 and 15 m. Full details are given in Bedwell *et al.* (1975), Medler (1977), and Jones (1979, 1982).

The current meters recorded mean peak speeds of 1.15 and 1.3 m s^{-1} during spring tides at new and full moon, respectively, and 0.8 m s^{-1} at the intervening neaps. Mean directions of the north-going and south-going tides were 0–12° and 182–193°, respectively, with a mean angular deviation (Batschelet, 1981) of 11°–26°. Speeds and directions were consistent with Admiralty predictions, which are averaged to take account of the regular diurnal, fortnightly, and seasonal differences in tidal range. Vertical variation was limited to the expected reduction in speed associated with the bottom boundary layer. Times of slack water generally differed by no more than 20 min from the predicted time and the differences in the times of slack water recorded by the upper and lower current meters did not exceed 15 min.

In January and October 1975, near-bed current measurements were made off Southwold by our colleague R. R. Dickson using five Savonius rotors fixed at different heights in the bottom boundary layer. The five stations (Fig. 1) were inshore of the tracks of cod 4, 5, 6, and 7, and most of track 9, but the results can reasonably be taken as indicative of the bottom boundary layer conditions for these tracks. Dickson found a linear relationship $U_{100}=0.88\ U_{700}$ ($r=0.95$, $n=123$), where U_{100} is the speed (cm s^{-1}) of the tidal stream measured at 1 m above the seabed with a Savonius rotor and U_{700} is the speed recorded at 7 m above the seabed with a direct-reading current meter. A similar relationship $U_*=0.073\ U_{100}$ ($r=0.96$, $n=150$) was found between U_{100} and the shear velocity U_* (an index of the deceleration of the current close to the seabed), where $U_*=(\tau/\rho)^{0.5}$, ρ is the density of the fluid, and τ is the shear stress on the bottom (e.g. Dyer, 1980).

Track plotting

Horizontal and vertical fish tracks were plotted by computer, using programs that allowed selected portions of the track to be enlarged as required. The horizontal track-plotting program converted Decca readings to latitude and longitude and corrected the computed position of the ship to that of the fish, using the range and bearing of the tag from the ship measured with the sonar. This program, which was validated against a large-scale hand plot of the track of cod 9, calculated distance (km), and direction (°T) between each successive position of the fish, together with speed over the ground and cumulative track distance. Obvious position fixing errors, which occurred because of incorrect Decca lane identification during adverse atmospheric conditions, were removed from the tracks. The scale of the remaining variable Decca errors has been discussed above; the much smaller fixed errors were ignored.

Speed and direction of fish through the water

The speed and direction of cod 4, 5, 6, 7, and 9 through the water were calculated using the resultant vector of the fish over the ground between successive Decca fixes and the tidal stream vector for the same 15-min period, interpolated from the current meter measurements. The behaviour of several other fish could be deduced from the ground track alone, using the predicted speed and direction of the tidal stream derived from appropriate Admiralty tidal stations and correcting for the systematic variation in speed through the spring–neap cycle.

For tracks 4, 5, 6, and 7 (Figures 3–6), the speed and direction of the tidal stream were taken directly from measurements made by rig 1 (Fig. 1). For cod 9 (Fig. 7), which remained at depths between 10 and 20 m, a linear interpolation was used to obtain the near-surface tidal stream vector at successive positions along the track between rigs 2 and 3. The speed of the near-surface tidal current at the inshore end of the track was estimated by raising the speed recorded by the single near-bed current meter on rig 2 by the ratio of the speeds recorded by the upper and lower current meters on rig 3.

The speed and direction of cod 7 through the water was also estimated using data recorded in 1980. This was done to assess the scale of error introduced by extrapolating the data from the single rig in 1974 over the whole of the tracks of cod 4, 5, 6, and 7. Through-water tracks were calculated using the data from rigs 5 and 6 separately and compared with a third track calculated using interpolated data (Fig. 14b).

The following convention was adopted to allow for the deceleration of the tidal stream with depth. For a fish swimming at any depth down to 20 m, the speed and direction of the water current were assumed to be that measured by the upper current meter. For a fish swimming below 20 m the current vector was assumed to be that measured by the lower meter. For a fish swimming at a height of less than 3 m above the seabed the speed of the current was assumed to be that at a height of 50 cm (U_{50}) calculated from $U_{50}=U_{100}-1.73\ U_{*}$, where $U_{*}=0.06\ U_{700}$ (see above). The equation for U_{50} was derived from the von Karman–Prandtl equation $u=u_{*}/\kappa \ln(z/z_0)$ (e.g. McCave, 1973; Dyer, 1980), where z and z_0 are height above bottom and roughness length, respectively, and von Karman's constant $\kappa=0.4$. The speed at a height of 7 m (U_{700}) was taken to be the speed measured by the lower current meter at a height of 8 m above the bottom, an assumption that overestimated U_{50} by approximately 2%.

The choice of the 3-m height was determined by the performance of the stabilization equipment of the sonar, which limited elevation (bearing) resolution to 1° and defined an envelope within which it was not possible to measure the angular separation of the tag signal from the seabed echo. The tracking range was typically 120 to 250 m (mean 175 m ± S.D. 30 m) and the mean height of the corresponding 1° envelope was 3 m (S.D. 0.6 m).

Although it was not possible to measure the height above the bottom of a fish within 1° of the seabed, it was possible to resolve whether the tag signal was contiguous with the bottom signal (*on the bottom*) or separated from it (*just off the bottom, JOB*) (Greer Walker *et al.*, 1978). Measurements with stationary tags at fixed heights above the seabed (carried out after the sector scanner had been transferred to RV "Corystes") demonstrated that a target had to be at a height of at least 2.5 m to be identified as JOB. Its signal would then be separated from the bottom echo by more than 1° at ranges up to 100 m and by less than 1° at greater ranges. The signal from a tag at a height of 1 m was not separated from the bottom echo at any range. The scale of the errors associated with the depth measurements made with the sector-scanning sonar are discussed by Arnold and Greer Walker (1992).

Results

Twenty-four cod (Table 1) were tracked in the southern North Sea (Fig. 1) during nine cruises between 1971 and 1979 and 12 tracks are analysed in detail here. Brief descriptions of the ground tracks are followed by an analysis of movements of fish through the water and a summary of vertical movements in relation to times of sunrise, sunset, and slackwater. Presentation of the results relies primarily on the figures and, for ease of interpretation, ground tracks are presented as well as though-water tracks, where appropriate. The two sets of horizontal track figures share common symbols.

Three patterns of movement were evident in the ground tracks. The three cod released at the surface behaved very differently from the 21 caged fish released at the seabed. Among the latter, fish released close to the coast showed different patterns of vertical and horizontal movement to those released further offshore. All tracks, though, were strongly influenced by the tidal currents.

Movements of fish over the ground

Fish released at the surface (cod 1–3) made no significant net movement over the ground. In contrast, many of the fish released from cages on the seabed (cod 4–24) showed consistent patterns of movement (Fig. 1). Five cod released off the coast of East Anglia moved offshore across the axis of the tidal streams. Three fish released to the south and east of the Norfolk Banks moved north by selective tidal stream transport. One fish tracked to the north of the Norfolk Banks moved along the tidal stream axis swimming for long periods in midwater, but making frequent visits to the seabed.

Undirected movements

Cod 1–3 were adapted to atmospheric pressure and were released at the surface. Each made a rapid dive on release but returned to the surface within 75 min. Subsequently, each fish descended slowly through the water column as it adjusted its depth of neutral buoyancy (Arnold and Greer Walker, 1992). These fish made little net movement over the ground and there was no consistent pattern in the direction of overall movement. Cod 1 (Fig. 1) showed a net movement of 17.3 km to the south (Table 1) because two nocturnal excursions into midwater coincided with south-going tides (Fig. 2a). Cod 2 showed a displacement of 14 km to the north after four south-going and four-and-a-quarter north-going tides (Table 1). Cod 3, which was tracked in the same location as cod 2, ended the track at almost the same latitude as that at which it started, after three south-going and three-and-a-quarter north-going tides.

Directed movements

Six of the eight cod released off the East Anglian coast (Table 1) moved away from the coast across the axis of the tidal stream, at the same time moving north and south over the ground with each successive tide (Fig. 1). Cod 4, 5, 6, 7, and 9 moved net distances of 15 to 20 km to the east. Cod 18, which was released much further offshore in deeper water, moved 6.5 km to the west (Table 1). All six tracks ended close to the longitude (2°12′E) of Smiths Knoll. Cod 23, which was released north of the Norfolk Banks, showed a net movement of 54.7 km to the east.

The track of cod 7. Cod 7 (Fig. 3), which was released at mid-morning during a south-going tide, covered a total distance over the ground of 65.8 km compared with a net distance of only 16 km (Table 1). The fish left the bottom 35 min after release and spent the next 19 h in

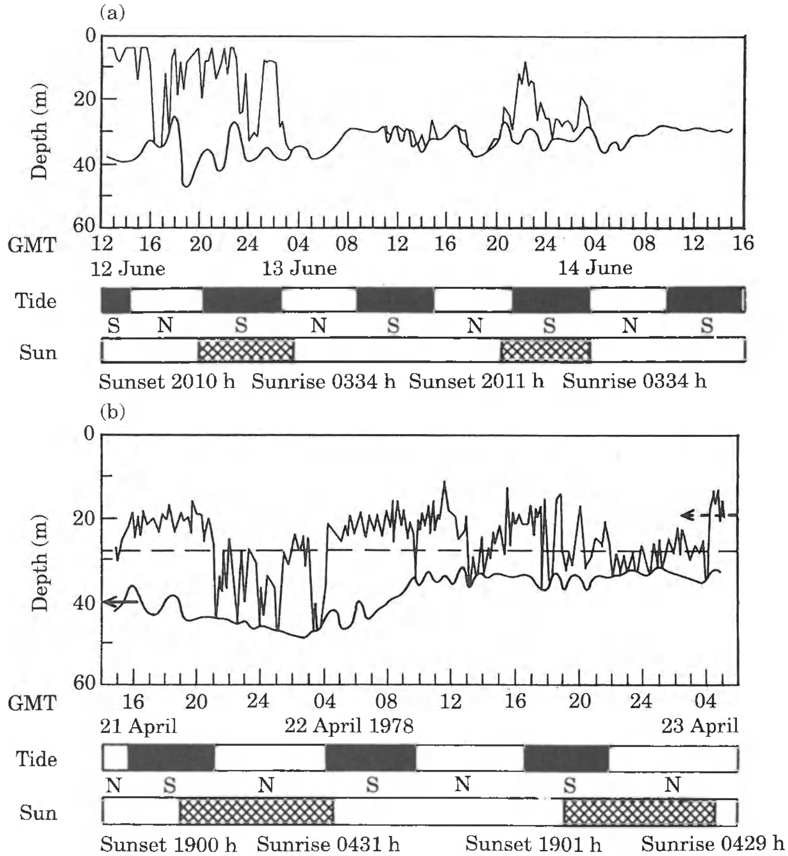

Figure 2. The depths of (a) cod 1 and (b) cod 23 in relation to the depth of the seabed, the direction of the tidal stream and times (GMT) of sunrise and sunset. Open bars indicate north-going (N) tides, black bars south-going (S) tides. In this and subsequent figures the bottom has been smoothed because of poor echoes at ranges beyond 200 m; the depth of the fish is shown as measured and is not smoothed. The solid arrow at 40 m in (b) indicates the predicted depth of neutral buoyancy when the fish was released from the cage; the dashed arrow at 19 m indicates the possible depth of neutral buoyancy at the end of the track. The long horizontal dashed line in (b) shows the upper limit of the free vertical range for the predicted depth of neutral buoyancy on release.

midwater, moving over the ground at average speeds of 50–90 cm s^{-1} (Table 2). During the second south-going tide (0400–0700 h), cod 7 was obviously moving north against the tide, as the distance (7.6 km) it moved to the south was only about half that of the tidal stream. The fish returned to the seabed at 0700 h when its ground track showed a sharp change of direction from 20° to 290°. A similarly abrupt change of direction occurred from 1300 h when cod 7 returned to the bottom after another period in midwater and swam to the north against a south-going tide.

Other East Anglian tracks. The remaining tracks in this area (cod 4, 5, 6, and 9) showed similar features (Table 1). Cod 4 (Fig. 4) and 9 (Fig. 7) both remained in midwater after release and their tracks resembled that of cod 7. The tracks of cod 5 and 6 (Figs 5, 6) were a little different. Both fish remained on the bottom for most of the first south-going tide after release and moved into midwater on the next north-going tide.

Cod 4, 7, and 9 all made substantially more ground to the east during north-going tides than they did during south-going tides, but this reflects the alignment of the tidal streams rather than a change in the behaviour of the fish. The mean track direction for the six complete south-going tides for these three fish was 173° (S.D. 6.5°); for the five north-going tides it was 26° (S.D. 8°). Cod 4, 5, 6, 7, and 9 moved net distances of 1 to 8 km normal to the axis of the tidal stream during single tides; the equivalent ground speeds were 4–40 cm s^{-1} (Table 2).

Cod 18 (Fig. 1; Table 1), which was tracked in the same general area but further offshore and well to the east of Smiths Knoll, behaved somewhat differently. This fish moved into midwater immediately after release and remained at a depth of 17 m (S.D. 1.9 m) for the entire track. It moved slowly westwards covering distances of between 1 and 4 km normal to the tidal stream axis during each of three complete tides (Table 2).

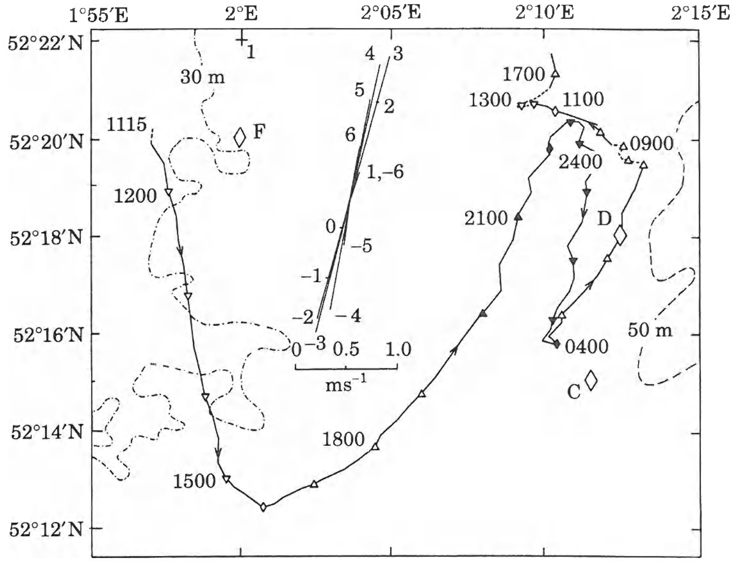

Figure 3. Track chart of cod 7 released on 28 April 1974. The position of the fish is plotted at 15-min intervals, except where shown otherwise, and hourly positions are indicated by triangles. Times (GMT) of predicted slackwater (to the nearest hour) are indicated by small diamonds. The solid line indicates periods when the fish was in midwater, the dashed line periods when the fish was on the bottom. Open triangles indicate north-going (△) and south-going (▽) tides during the day, closed triangles the corresponding tides at night. Isobaths from British Admiralty chart 1504 (1983). The insert and associated scale bar shows the tidal stream vectors predicted at tidal station F (large diamond) at spring tides for hourly intervals from 6 h before (negative values) to 6 h after (positive values) high water Dover (HWD). Minimal speeds (slackwater) were recorded by the top current meter on rig 1 (+) at 1546, 2216, 0416 and 1036 h.

The track of cod 23. Cod 23 (Table 1; Figs 2b, 8) was released near Markhams Hole (Fig. 1) in mid-afternoon shortly before slack water in an area where the tidal stream axis is south-east and north-west. This fish left the seabed immediately after release and remained in midwater for the duration of the first south-east-going tide, before returning briefly to the bottom at high-water slack. It spent the subsequent north-west-going tide in midwater, but at a lower mean depth than on the previous tide, and went to the bottom on five separate occasions (Fig. 2b). This pattern of behaviour was maintained for the rest of the track with the fish moving on and off the bottom at the beginning and end of each south-going tide and visiting the bottom several times during each north-going tide. During the last north-going tide cod 23 was recorded as being JOB at 2235, 2245, 2300, and 2315 h.

Between its release and 0400 h 22 April cod 23 swam north-east a net distance of 20.9 km, but covered a total distance of 28.7 km as it was displaced first south-east and then north-west by the tidal stream. From 0400–2400 h 22 April, cod 23 moved east by south a net distance of 35.4 km. Its speed over the ground was enhanced by the south-going tidal stream between 0500–0900 h and 1600–2100 h. From 1000–1600 h, and again from 2200 h until the end of the track, the rate of movement over the ground was greatly reduced by the north-going tidal stream. The north-easterly displacement between 1400–1600 h 22 April was consistent with the predicted tidal stream vectors for 5 and 6 h after high water Dover (Fig. 8).

Selective tidal stream transport

Three of the nine fish tracked south and east of the Norfolk Banks showed selective tidal stream transport and moved net distances of more than 40 km north along the tidal stream paths. Cod 11 adopted this pattern of behaviour on release; cod 10 and 20 initially behaved differently.

The track of cod 10. Cod 10 (Table 1; Figs 9a, 10a) was released at midday during a north-going tide. It moved immediately into midwater, where it remained for the first three tides, apart from a descent at sunset on the first evening, when it went briefly to the bottom, and another at sunrise the next morning (Table 6), when it was within 3 m of the seabed. After another short period in midwater it went to the bottom at 0625 h 25 April, approximately 1 hour after slack tide. During the first three tides cod 10 moved north and south in the direction of the tidal stream. During the fourth and fifth tides it showed selective tidal stream transport, moving 20 km to the north between 1100 and 1700 h 25 April. For the rest of the track cod 10 moved about locally over the southern tip of the Knoll Bank, never moving very far above the bottom.

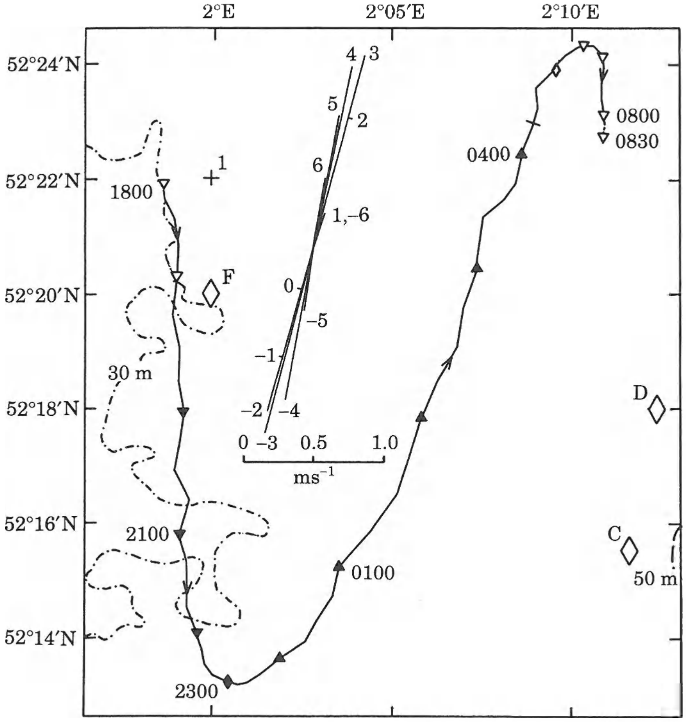

Figure 4. Track chart of cod 4 released on 21 April 1974. The cross ticks between 0400–0500 h indicate times at which the fish went briefly to the bottom; other details as in Figure 3. Slackwater was recorded by the top current meter on rig 1 (+) at 2306 and 0516 h.

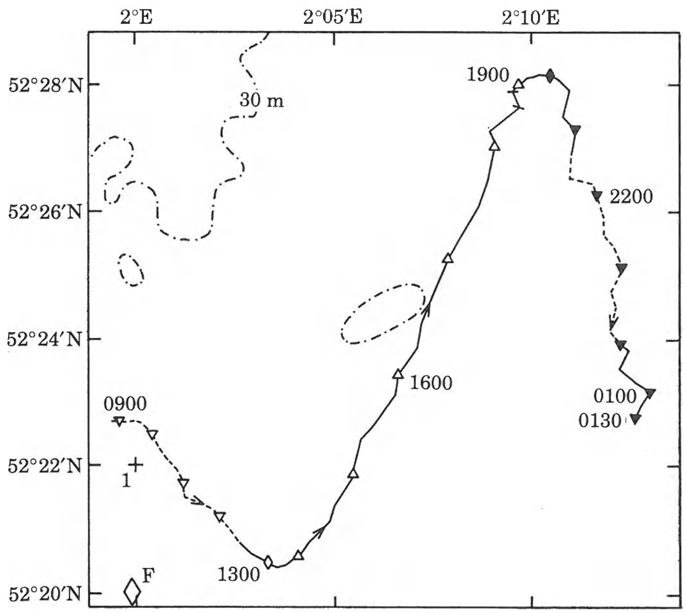

Figure 5. Track chart of cod 5 released on 25 April 1974. Details as in Figure 3. Slackwater was recorded by the top current meter on rig 1 at 1316 and 1926 h.

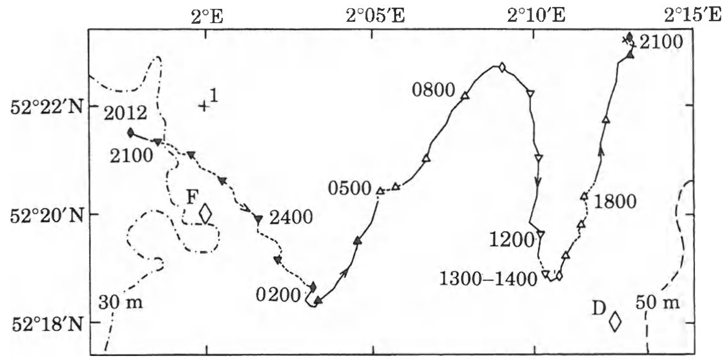

Figure 6. Track chart of cod 6 released on 26 April 1974. Details as in Figure 3. Slackwater was recorded by the top current meter on rig 1 (+) at 2016, 0236, 0836, 1446, and 2106 h.

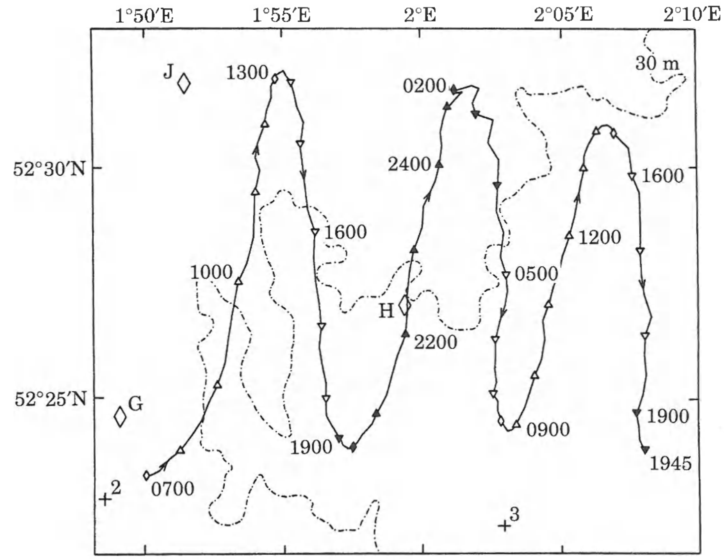

Figure 7. Track chart of cod 9 released on 21 April 1975. Details as in Figure 3. Slackwater was recorded by the single current meter on rig 2 at 0648 and 1308 h and by the top current meter on rig 3 at 1942, 0231, 0832, 1442, and 2042 h.

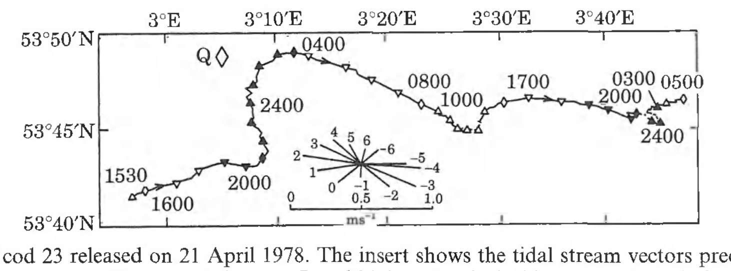

Figure 8. Track chart of cod 23 released on 21 April 1978. The insert shows the tidal stream vectors predicted for spring tides at tidal station Q. Symbols and conventions as in Figure 3. Local high water slack tide occurs at 1 h before HWD, local low-water slack at 6 h after HWD. Predicted times of HWD: 2207 h 21 April; 1024 and 2242 h 22 April; 1101 h 23 April.

The track of cod 11. Cod 11 (Table 1; Figs 9b,10b), which was released during a north-going tide in the afternoon, also moved into midwater immediately after release. It, too, moved north by selective tidal stream transport, although its vertical movements were not synchronized with slack water. Cod 11 remained on the bottom for only 2–3 h during each of the two south-going tides and was displaced to the south by these tides when it was in midwater. It none the less moved substantial distances (13, 24, and 17 km) northward during the three north-going tides.

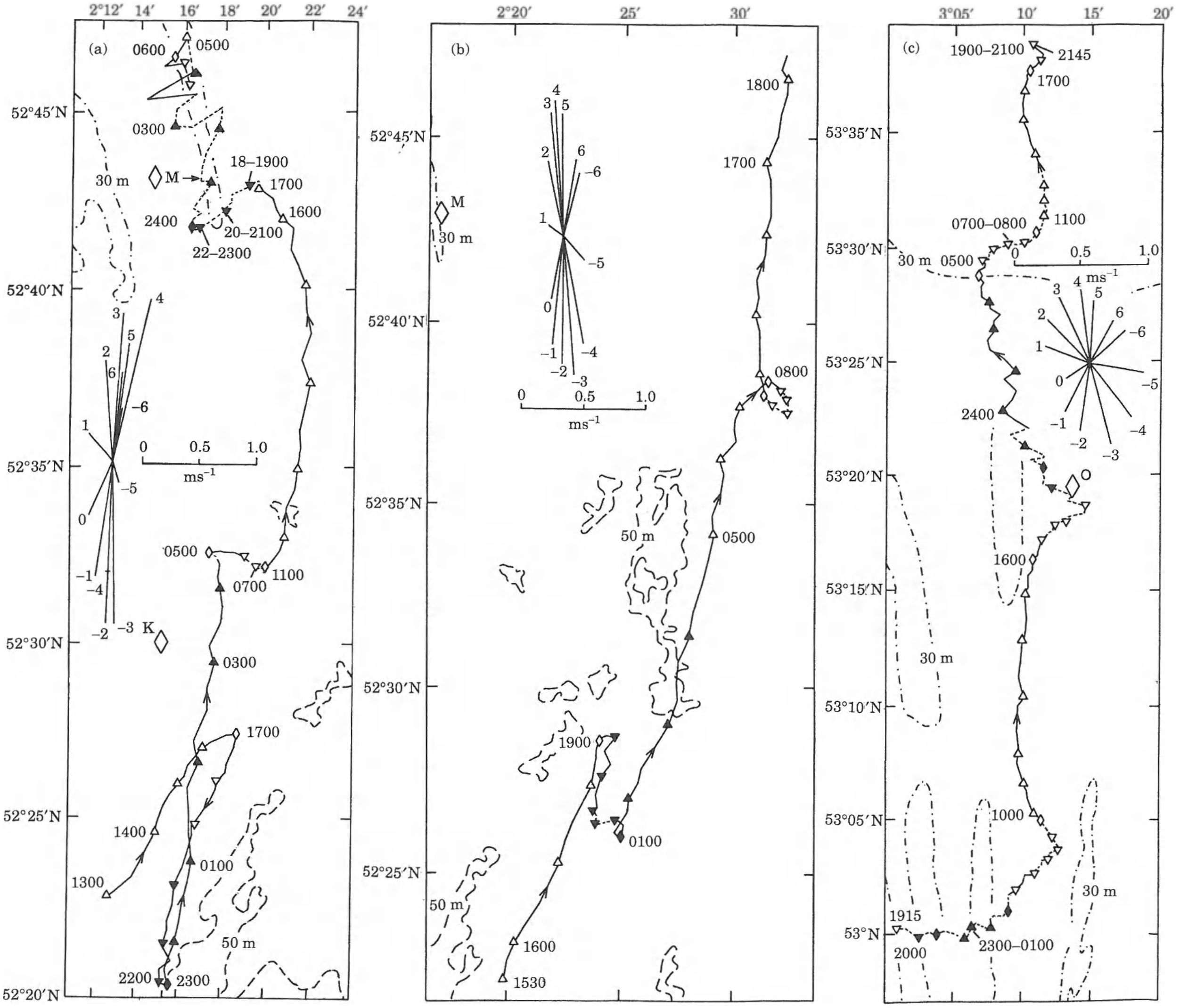

Figure 9. Track charts of (a) cod 10, (b) cod 11, and (c) cod 20 released on 24 and 27 April 1975 and 30 May 1977, respectively. Isobaths from British Admiralty charts 1504 (a, b) and 1505 (c). The inserts show the tidal stream vectors predicted for spring tides at tidal stations, K, M, and O, respectively. Symbols and conventions as in Figure 3.

The track of cod 20. Cod 20 (Table 1, Figs 9c,10c), which was released in the evening towards the end of a south-going tide, remained on the bottom for most of the first 12 h. It moved initially eastwards for 11.2 km (1915–0300 h), then north-eastwards for 6.5 km (0300–0700 h) and finally north-westwards for 2.8 km (0700–0900 h). The fish moved briefly into midwater at 0230 h and then made a more extensive excursion from 0330–0500 h. Thereafter, cod 20 exhibited selective tidal stream transport and moved into midwater during each of three successive north-going tides. It returned to the seabed during the intervening south-going tides but still progressed to the north. The duration of the third midwater excursion was similar to that of the north-going tide; the durations of the second and fourth excursions were longer and shorter, respectively, than the tide by about 2 h. The successive displacement of cod 20 over the ground to the east and back to the west during these three tides was consistent with the shape of the local tidal stream ellipse (Fig. 9c).

Movements of fish through the water

Although the tracks of cod 1, 2, and 3 could be accounted for primarily by passive drift, the ground tracks of most other fish were strongly influenced by the movement of the fish through the water. Substantial differences were also observed between the behaviour of fish in midwater and fish close to the seabed.

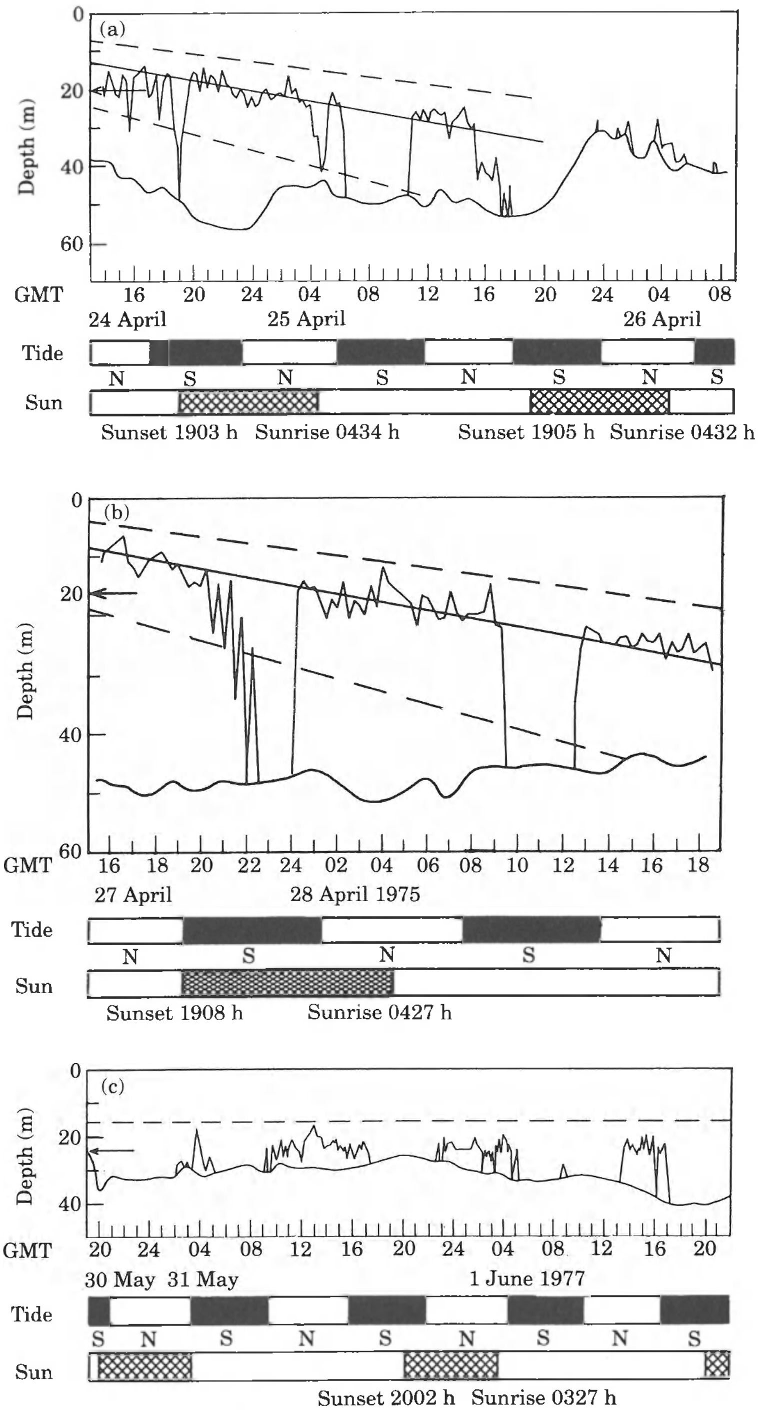

Figure 10. The depth of (a) cod 10, (b) cod 11, and (c) cod 20 in relation to the direction of the tidal stream and other environmental factors. The solid line in (a) and (b) indicates the mean rate of descent and the dashed lines the corresponding upper and lower limits of the free vertical range for a fish in neutral buoyancy at the mean depth (Arnold and Greer Walker, 1992). The horizontal dashed line in (c) shows the upper limit of the free vertical range for the predicted depth of neutral buoyancy on release. Other details as in Figure 2.

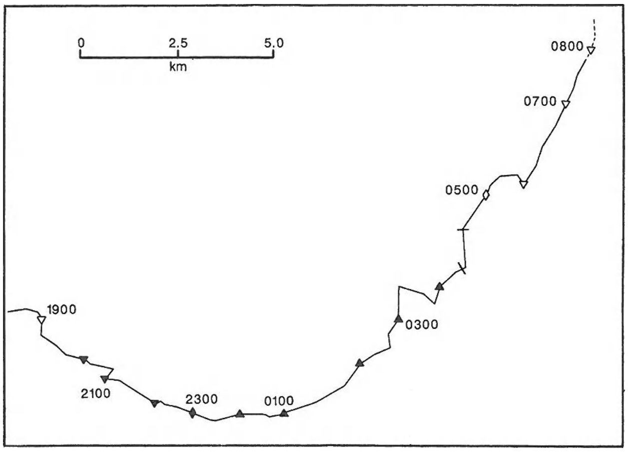

Figure 11. Progressive vector plot of the movements of cod 4 through the water for successive 15-min periods. Dashed lines and cross ticks indicate when the fish was on the bottom. Distance is indicated by the 5-km scale bar. Symbols as in Figure 3.

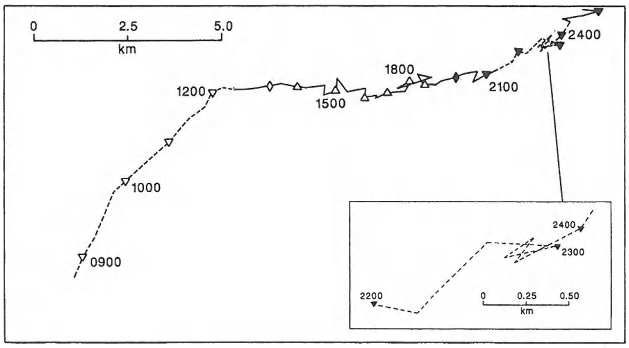

Figure 12. Progressive vector plot of the movements of cod 5 through the water. Symbols as in Figures 3 and 11.

Passive drift

The net movement of cod 1, 2, and 3 over the ground was in each case less than 20 km (Table 1), but the fish moved to and fro with each successive tide and the total distances covered during the three tracks were, respectively, 78, 162, and 112 km. These movements appeared to be largely, although not entirely, attributable to those of the tidal streams, as can be shown by a comparison of the fish tracks with those of a parachute drogue and seabed drifter tracked in the same general area in June 1971 (Harden Jones *et al.*, 1973). The drogue and the drifter each transcribed a long narrow ellipse, whose orientation and dimensions – allowing for bottom friction in the case of the drifter – were consistent with Admiralty tidal stream predictions. The ground tracks of cod 2 and 3 followed a similar pattern, although for the first three legs of its track cod 3 swam downstream at a speed about half as fast again as the tidal stream. A component of its swimming was also directed across the tidal axis because the ellipse (Fig. 1) was more rounded than that of the parachute drogue. Cod 1 behaved similarly for the first 8 h after release and moved to the east across the tide. Otherwise, the ground speeds of all three fish were close to those predicted for the tidal current and for most legs the track direction was within 15° of the tidal stream axis.

Active movements

Cod in midwater behaved differently from cod on the bottom. Fish in midwater were observed to swim in a consistent direction for periods of several hours, but these portions of the tracks were also characterized by: (1) large changes in direction occurring gradually over long periods; (2) sustained movements across the axis of the tidal stream; (3) periods of reduced speed, and possibly circling behaviour; and (4) no change in heading when the tidal stream reversed. In contrast, cod on or close to the seabed swam against the tide for extended periods without any large change in heading. And fish going to the seabed after a long period in midwater made rapid changes in heading to oppose the prevailing tide, sometimes reversing direction completely.

Initial heading on release. Two patterns of movement are evident in the tracks of the five fish that moved east

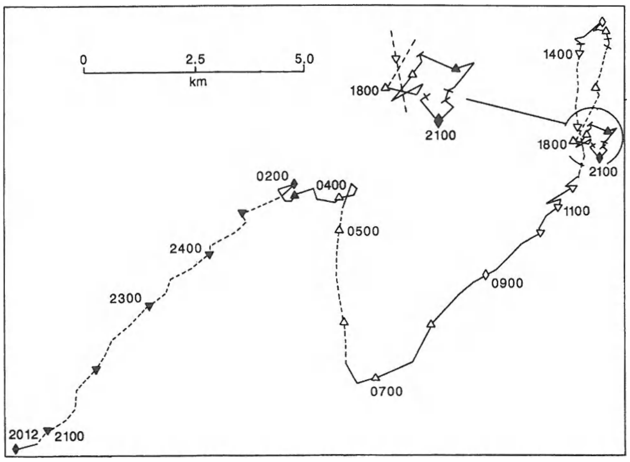

Figure 13. Progressive vector plot of the movements of cod 6 through the water. Symbols as in Figures 3 and 11.

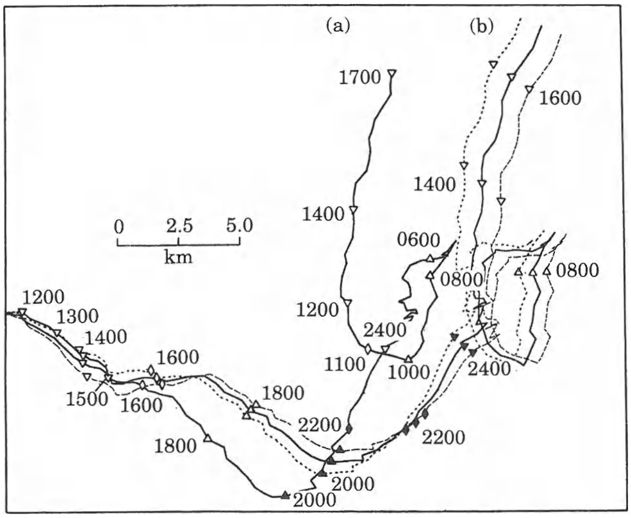

Figure 14. Progressive vector plots of the movements of cod 7 through the water estimated from tidal stream vectors measured by (a) rig 1 in April 1974 during the track and (b) rigs 5 and 6 in April 1980. The progressive vectors in (b) were calculated using data interpolated between the two rigs (——) and the data from the two rigs separately (···· and ----). The divergence between the through-water tracks in (a) and (b) is produced by a difference in the direction of rotation of the tidal stream over slackwater in the two years. Anti-clockwise rotation in 1974 was accompanied by east-going tidal stream vectors, clockwise rotation in 1980 by west-going tidal stream vectors. The application of the 1980 tidal current data to the 1974 ground track results in an overestimate of the easterly swimming speed of the fish between 1500–1700 h and 0500–0700 h and a corresponding underestimate of the westerly swimming speed between 1000–1200 h. Symbols as in Figures 3 and 11.

away from the East Anglian coast. The two fish that remained on the bottom (cod 5 and 6) swam to the north-east against the tide; the three fish (cod 4, 7, and 9) that moved into midwater swam to the east or south-east across the axis of the tidal stream.

Cod 5 and 6 (Figs 12, 13) remained on the bottom for 3 (0845–1230 h) and 5 (2045–0145 h) hours, respectively, after release. Assuming they were swimming at a height of 50 cm above the seabed and there were no topographic features to distort the logarithmic speed profile in the bottom boundary layer, these fish headed at 45° and 42° through the water (Table 3b), each course making an angle of about 140° to the mean recorded direction (186° ± S.D. 20 and 183° ± S.D. 4, respectively) of the tide. Table 4 shows that, provided each fish was at a height of 25 cm or more, its estimated direction through the water is unlikely to have been in error by more than 10° either way, regardless of its height in the bottom boundary layer.

Cod 7 (Fig. 14a; Table 3) initially headed east on the bottom for a short period after release, but subsequently left the bottom at 1130 h and swam along a mean

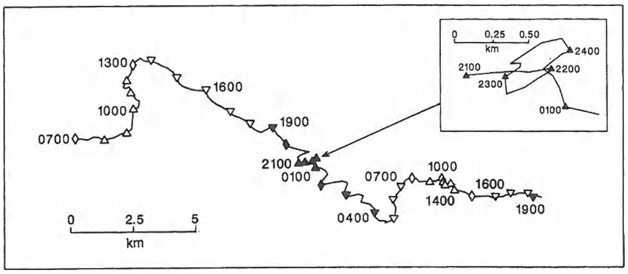

Figure 15. Progressive vector plot of the movements of cod 9 through the water; symbols as in Figures 3 and 11.

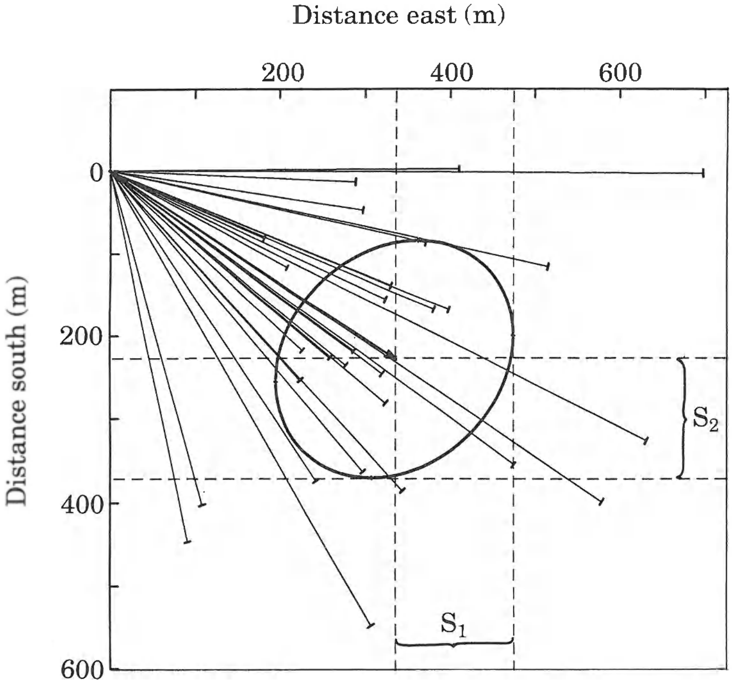

Figure 16. Through-water vectors for cod 7 for successive 15 (or 30) min periods from 1130–1930 h, 28 April 1974. The standard ellipse and mean vector (405 m, 124°, r=0.33) are shown, together with the standard deviations s_1 and s_2 (Batschelet, 1981).

bearing of 124°. It maintained this heading for 8 h, while the tide flowed first to the south and then to the north (mean recorded directions 186° and 14°). For most of this period the fish was swimming at a depth of less than 10 m from the surface. Figure 14b shows that the estimated heading of the fish is unlikely to have been in error by more than 5° in either direction as the result of extrapolating the current meter measurements from rig 1.

Cod 4 and 7 both swam to the east for a short period after release (Figs 11, 14a). Cod 4 then adopted a similar course to cod 7 and headed 118° from 1915–2315 h (Table 3) when the mean direction of the tide was 190°. Cod 9 (Fig. 15), in contrast, turned north (6°) for the remainder of a north-going tide (mean direction 13°), until low-water slack at 1300 h.

Subsequent midwater headings. None of the five fish that moved offshore maintained the same heading for the whole of the track. On leaving the bottom, cod 5 and 6 (Figs 12, 13; Table 3a) both turned to the east for the duration of the ensuing midwater period. On its second midwater excursion (0700–1200 h), cod 6 headed north-east again, and cod 4 and 7 (Figs 11, 14; Table 3a) adopted similar directions from 0100 and 2030 h, respectively. Cod 9 (Fig. 15), in contrast, adopted a south-easterly heading for much of its track from 1300 h onwards.

Subsequent headings on the bottom. Cod 5, 6, and 7 all went to the bottom again later in the track and on each occasion headed against the tide. Cod 6 (Fig. 13; Tables 3, 4) swam south (177–182°) during a north-going tide between 0445–0630 h; north (2–3°) against a south-going

Table 2. Ground speeds of cod that showed directed movements across the axis of the tidal stream: for cod 9 this axis was 5–185° (T); for the other fish it was 13–193° (T).

Cod	Time interval (GMT)	Time in midwater (%)	North-going (N) or south-going (S) tidal stream	Net movement over the ground			Net movement normal to tidal stream axis	
				Direction (°T)	Distance (km)	Speed (cm s^{-1})	Distance (km)	Speed (cm s^{-1})
4	1800–2300	100	S	172	16.3	91	5.7	31.6
	2300–0600	100	N	29	23.5	93	6.7	26.6
	0600–0830	70	S	168	2.9	32	1.2	13.6
5	0845–1315	6	S	132	6.2	38	5.4	33.4
	1315–1945	100	N	29	16.4	70	4.6	19.6
	2015–0130	20	S	164	10.4	55	5.1	26.8
6	2012–0230	8	S	134	8.6	38	7.4	38.7
	0230–0900	64	N	40	10.7	46	5.0	21.4
	0900–1445	90	S	166	7.5	36	3.3	15.9
	1445–2100	72	N	19	8.9	40	0.9	4.2
7	1115–1600	88	S	164	15.0	88	7.4	43.4
	1600–2300	100	N	39	19.0	75	8.3	32.8
	2300–0400	100	S	184	8.5	47	1.3	7.4
	0400–0700	100	N	27	7.6	70	1.8	16.5
	0700–1300	46	N–S	298	5.2	24	5.0	23.3
	1300–1700	12	S	48	1.7	12	1.0	7.1
9	0700–1330	100	N	20	16.1	69	4.1	17.3
	1330–1945	100	S	170	14.4	64	3.7	16.6
	1945–0215	100	N	20	14.5	62	3.7	15.8
	0215–0815	100	S	174	13.0	60	2.4	11.2
	0815–1430	100	N	20	12.2	54	3.1	13.7
	1430–1945	100	S	173	12.3	65	2.5	13.0
18	0821–1300	100	N	2	6.1	36	1.2	7.0
	1300–1900	100	S	198	9.6	44	0.9	4.0
	1900–0100	100	N	353	11.9	55	3.9	18.2
	0100–0700	100	S	192	10.6	49	0.2	0.9

tide from 1230–1400 h; and south (196°) against a north-going tide between 1615–1800 h. The corresponding directions of the tidal stream measured in the lower half of the water column were 014°, 182°, and 014° (S.D. 3–4°). Cod 7 (Fig. 14a; Table 3) behaved similarly, opposing north- and south-going tides (recorded directions 9° and 184°) when on the bottom between 0700–0930 and 1215–1630 h, and swimming in directions of 205–211° and 9–10°, respectively. All five examples of swimming against the tide occurred during daylight.

Other movements opposed to the tidal stream. There were further examples of fish heading the tide during the tracks of the three cod (cod 10, 11, and 20) that showed selective tidal stream transport. Most occurred while the fish were on the bottom; two occurred while they were in midwater.

Cod 20 continued to move north during each of three opposing south-going tides. It covered distances of 7.9 (0300–0900 h), 7.5 (1600–2200 h), and 5.8 km (0400–1000 h) in a northerly or north-easterly direction between successive slack waters (Fig. 9c), compared with predicted tidal stream excursions of 7–7.5 km in a southerly direction. The fish remained on the bottom for most of these periods, the greater part of which occurred by day.

Cod 10 swam north in midwater against the first south-going tide, before adopting tidal stream transport at 2300 h (Fig. 9a). Apart from one brief visit to the bottom at sunset (Fig. 10a), the fish was in midwater after dark (1700–2300 h) and moved 13.7 km to the south, compared with a predicted tidal stream excursion (Station K) of approximately 20 km in the same direction. On the next south-going tide (0500–1100 h) cod 10 held its ground against the opposing stream during daylight, although making a small movement to the east. On the third south-going tide (1730–2400 h), which occurred after dark, the fish lost ground and moved a net distance of 5 km to the south-west. During both tides cod 10 was on the bottom.

Cod 11 (Fig. 9b) behaved similarly, moving a comparable distance to the south-east during the first south-going tide, which occurred at night (1900–0100 h), and rather less during second south-going tide, which occurred by day (0800–1300 h). Cod 11 was on the bottom for several hours during each of these two tides (Fig. 10b).

Table 3. Mean swimming speeds and directions of cod 4, 5, 6, 7, and 9 through the water for consecutive 15-min periods estimated from the ground tracks of the fish (Figs 3, 4, 5, 6, and 7) and simultaneous measurements of the speed and direction of the tidal stream made by recording current meters. Fish recorded as being *on the bottom* (tag signal contiguous with bottom echo) are assumed to be swimming at a height of 50 cm.

Cod	Time interval (GMT)	Day (D) or night (N)	n	Mean direction (°T)	Angular deviation (°T)	Mean speed (cm s^{-1})	S.D.	Mean specific speed (L s^{-1})	S.D.
(a) Fish in midwater									
4	1915–2315	N	15	118	34	35.6	17.9	—	—
	0100–0300	N	8	046	24	56.7	23.8	—	—
	0600–0800	D	8	027	06	49.1	14	—	—
6	0700–1200	D	19	045	33	39.7	24	0.79	0.48
7	1130–1930	D	32	124	19	48	14.1	0.80	0.24
	2030–0030	N	16	025	31	54.6	22.2	0.91	0.37
	1000–1200	D	7	307	17	44.9	17.5	0.75	0.29
9	0700–0900	D	12	085	16	30	8.7	0.44	0.13
	0900–1310	D	25	006	40	24.3	11.2	0.35	0.16
	1310–1900	D	35	115	26	32.7	8.4	0.47	0.12
	1900–0440	N	58	136	55	28	18.2	0.50	0.26
	0440–0800	D	20	031	33	21.2	9.7	0.31	0.14
	0800–1800	D	60	100	45	17.7	9.2	0.26	0.13
(b) Fish on the bottom									
5	0845–1230	D	15	045	19	52.1	16.5	—	—
6	2045–0145	N	20	042	24	56.7	16.1	0.93	0.32
	0445–0630	D	7	179	7	55.8	4.2	1.12	0.08
	1230–1400	D	6	002	10	51.4	10.8	1.03	0.22
	1615–1800	D	7	196	19	38	11.3	0.76	0.23
7	0700–0930	D	10	208	29	51.6	16.8	0.86	0.28
	1215–1630	D	17	010	18	49.9	11.7	0.83	0.20

Like cod 10, cod 7 also opposed a south-going tide when swimming in midwater after dark. It swam NNE between 2200–2400 h, after swimming in the same direction for the previous 2 hours, during the decelerating phase of the previous tide (Fig. 14).

Downstream movements. Downstream movements in midwater during the north-going tide occurred, day and night, during the tracks of cod 4 (0200–0500 h), cod 5 (1700–1930 h), cod 6 (0700–0830 h), cod 7 (2000–2200 h), and cod 9 (0900–1300 h).

Similar behaviour occurred with one of the fish that showed selective tidal stream transport. Cod 10 and 11 added little to the net distance moved over the ground during the transporting tide, but cod 20 appears to have continued to swim to the north when it was in midwater during the north-going tide (Fig. 9c; Table 5). It covered net distances of 21.1 and 16.5 km to the north, respectively, between 0900–1600 and 2200–0400 h, compared with predicted tidal stream excursions (Station 0) of 9–9.4 km. The differences between the observed and predicted excursions suggests that fish was swimming through the water at speeds of 0.3–0.5 m s^{-1} (0.5–0.7 L s^{-1}). The shorter distance (13.3 km) over the ground covered during the last north-going tide (1000–1600 h) reflects the fact that cod 20 was in midwater for less than 4 h during this tide (Fig. 10c).

Changes of direction. There were several large changes of swimming direction during the tracks of cod 4, 5, 6, 7, and 9. The largest and fastest were associated with visits to the seabed during midtide, when the fish turned to head into the tidal stream. Others, which involved smaller angles, occurred as the fish left the bottom, or shortly after it had moved into midwater. Large changes in direction that occurred in midwater were much slower and usually spanned several hours.

Cod 7 made a slow left turn of approximately 90° between 1900–2100 h after 7.5 h in midwater. The turn began at sunset and occurred during the middle of a north-going tide. The fish subsequently adopted a mean heading of 25° (Table 3) and remained in midwater for a further 10 h (Fig. 14a). Cod 4 made an even more gradual left turn, also while swimming in midwater during a north-going tide. This fish (Fig. 11; Table 3) changed heading over a 2-h period at night (2300–0100 h) from a course of 118° (1915–2315 h) to a course of 46° (0100–0300 h), which it maintained for the rest of the track. In each case the slow left-hand turn brought the fish onto a course that was broadly downtide. A similar, but rather sharper, change to a north-easterly heading was evident in the track of cod 6 (Fig. 13) between 0630 and 0700 h. Cod 9 (Fig. 15) made large changes of direction in midwater at 0900 and again at

Table 4. Mean swimming speeds and directions of cod 6 through the water calculated for the four periods (Fig. 6) when the fish was recorded as being *on the bottom* (tag signal and bottom echo contiguous) assuming five different heights for the fish in the bottom boundary layer. The centre line of a swimming cod of 50–70 cm length (L) is unlikely to get closer than 10 cm to the bottom as it will have its median fins at least partially erect; with fully erect fins the maximum vertical dimension of the fish is 0.26 L (Haslett, 1962).

Period (GMT)	n	Height above bottom (cm)	Mean direction (°T)	Angular deviation (°T)	Mean speed (cm s^{-1})	S.D.	Mean specific speed (L s^{-1})	S.D.
2045–0145	20	300	036	19.6	54.9	16.2	1.10	0.32
		100	037	20.6	52.6	16.1	1.05	0.32
		050	042	23.6	46.7	16.1	0.93	0.32
		025	049	27.3	41.4	16.6	0.83	0.33
		010	070	36.8	35.9	17.3	0.72	0.35
0445–0630	7	300	182	5.8	67.4	4.4	1.35	0.09
		100	181	6.1	64.3	4.4	1.29	0.09
		050	179	7.0	55.8	4.1	1.12	0.08
		025	177	8.2	47.5	4.0	0.95	0.08
		010	172	10.8	36.4	3.7	0.73	0.07
1230–1400	6	300	003	9.8	59.2	12.3	1.19	0.25
		100	003	10.0	57.2	11.8	1.14	0.24
		050	002	10.4	51.4	10.8	1.03	0.22
		025	002	11.0	45.6	10.6	0.91	0.21
		010	001	12.3	37.8	11.6	0.76	0.23
1615–1800	7	300	196	13.0	48.8	12.0	0.98	0.24
		100	196	14.3	45.9	11.8	0.92	0.24
		050	196	19.3	38.0	11.3	0.76	0.23
		025	196	27.8	30.4	10.2	0.61	0.20
		010	205	41.6	21.4	7.5	0.43	0.15

1300 h, the first during mid-tide, the second at low water slack; a third sharp turn at 0445 h occurred during mid-tide, shortly after sunrise.

Changes of direction of approximately 180° were observed during the tracks of cod 6 and 7, when the fish went to the seabed during midtide in daylight. Cod 7 (Fig. 14a) returned to the bottom at 0700 h during a north-going tide and immediately reversed its direction to a mean heading of 208° (Table 3). Cod 6 (Fig. 13) showed similar behaviour between 0400–0500 h. Comparable, although smaller, changes in swimming direction occurred during the tracks of cod 5 and 6 as, or shortly after, the fish left the bottom during daylight. Cod 5 (Fig. 12) made a turn of approximately 45° while it was still on the bottom at 1215 h. Cod 6 (Fig. 13) made a 90° turn to the left shortly after it left the bottom between 0630 and 0700 h.

Maintenance of heading. Cod 23 appears to have maintained a consistent heading for two long periods between release and 0400 h 22 April and between 0400–2400 h in the same day, heading north-east for 13 h and south-east for 20 h (Fig. 8). It made several visits to the seabed between these times but between 0335–2205 h 22 April the fish remained in midwater for four periods, during each of which it showed little deviation in heading from the overall course. These four periods (Fig. 2b) lasted for 6.2, 3.3, 4.1, and 3.75 h, respectively.

The ability of cod to maintain a course in midwater for several hours was also evident in the tracks of several other fish. Some measure of the consistency with which they did so can be obtained from an examination of the progressive vector plots of cod 4, 5, 6, 7, and 9 (Figs 11–15) and the angular deviations of the mean headings for selected periods (Table 3). The data for cod 7 from 1130–1930 h suggest that cod in midwater by day may be able to maintain a consistent heading for periods of up to 8 h without deviating from the overall course by more than ±40–45° (Fig. 16). Cod 4 performed similarly in midwater at night, although only for 2 h (0100–0300 h). Somewhat greater angular deviation was evident in the other examples. Cod swimming against the tide close to the seabed appeared to be able to hold a compass heading with a comparable degree of precision (Table 3b).

Swimming speeds. Cod 4, 6, 7, and 9 maintained average swimming speeds of between 20–60 cm s^{-1} (0.3–0.9 L s^{-1}) when in midwater (Table 3a), and these estimates are unlikely to be in error by more than 2% as a result of extrapolating the current meter measurements from rig 1 over the whole of the tracks (Fig. 14b). Comparable speeds were estimated for fish 5, 6, and 7 on the bottom, assuming that they were swimming at a height of 50 cm (Table 3b). Different assumptions produced estimates that varied by ±20–30% depending on

Table 5. Net distances travelled by cod 10, 11, and 20 over the ground during the north-going transporting tide compared with the predicted tidal stream excursion.

Cod	Time interval (GMT)	Net distance of fish over ground (km)	Tidal station	Predicted tidal stream excursion (km)	Comments
10	1300–1700	10.7	K	12.0	Last 4 h of tidal stream
	2230–0500	22.9		21.8	
	1100–1800	19.9		21.8	
11	1530–1930	13.1	K	13.0	Last 4 h of tidal stream
	0100–0800	24.0		21.3	
	1330–1830	16.8		16.1	First 5 h of tidal stream
20	0900–1600	21.1	O	9.0	
	2200–0400	16.5		9.4	
	1000–1700	13.3		9.6	Fish in midwater 1330–1710 h

Table 6. Times of ascents and descents of cod 10 and 20 in relation to sunrise (SR) and sunset (SS) and to predicted times of local high (HWS) and low (LWS) water slack tide. Some excursions, which occurred during midtide and more than 1 h from sunrise or sunset (Fig. 10), have been excluded.

Cod	Ascent or descent	Time (GMT)	Time of predicted local HWS or LWS (GMT)		Time of ascent or descent before (−) or after (+) slackwater (min)	Time of sunrise or sunset (GMT)		Time of ascent or descent before (−) or after (+) SR or SS (min)
10	Descent/ascent	1910	—	—	—	SS	1903	+7
	Descent/ascent	0500	LWS	0525	−25	SR	0434	+26
	Descent	0625	LWS	0525	+60	—	—	—
	Ascent	1045	HWS	1125	−40	—	—	—
	Descent/ascent	1703	LWS	1746	−43	—	—	—
	Descent/ascent	1720	LWS	1746	−26	—	—	—
	Descent/ascent	1731	LWS	1746	−15	—	—	—
	Descent	1748	LWS	1746	+2	—	—	—
	Ascent/descent	2340	HWS	2346	−6	—	—	—
	Ascent/descent	0100	HWS	2346	+74	—	—	—
	Descent	0545	LWS	0610	−25	—	—	—
20	Ascent/descent	0230	—	—	—	SR	0328	−58
	Ascent/descent	0330	LWS	0325	+5	SR	0328	+2
	Ascent/descent	0338	LWS	0325	+13	SR	0328	+10
	Ascent	0340	LWS	0325	+15	SR	0328	+12
	Descent	0500	LWS	0325	+95	—	—	—
	Ascent/descent	0900	HWS	0925	−25	—	—	—
	Ascent/descent	0915	HWS	0925	−10	—	—	—
	Ascent/descent	0928	HWS	0925	+3	—	—	—
	Ascent	0932	HWS	0925	+7	—	—	—
	Descent	1726	LWS	1546	+100	—	—	—
	Ascent	2230	HWS	2146	+44	—	—	—
	Descent/ascent	2253	HWS	2146	+67	—	—	—
	Descent/ascent	0315	—	—	—	SR	0327	−12
	Descent/ascent	0440	LWS	0414	+26	—	—	—
	Descent	0510	LWS	0414	+56	—	—	—

whether the fish was higher or lower (Table 4) in the bottom boundary layer.

In contrast, there were several periods when fish in midwater swam slowly and occasions when they appeared to swim in circles. There was no obvious correlation of these events with any single environmental variable. Some occurred near slack water, others during midtide, some during the day, some at night. Cod 5 appeared to swim in circles between 1800–1900 h and again between 2200–2300 h (Fig. 12), and cod 6 behaved similarly between 0200–0300 h and 1800–1900 h (Fig. 13). Cod 9 appeared to describe a rather larger circle over a period of 3 h between 2200 and 0100 h (Fig. 15). Similar behaviour has been described in plaice (Harden Jones, 1981; Harden Jones and Arnold, 1982) and salmon (Greer Walker, unpublished observations) fitted with transponding acoustic compass tags.

Vertical movements

Most fish made rapid vertical movements at the beginning of the track and again at the beginning and end of each major excursion into midwater; some also showed a slow progressive increase in depth in midwater, which was maintained for several hours. The data were analysed by Arnold and Greer Walker (1992), who discussed the significance of both types of behaviour in relation to the hydrostatic function of the swimbladder.

Timing of ascents and descents

For those fish that exhibited selective tidal stream transport, rapid ascents and descents were generally associated with times of slack water; for several other fish they occurred at, or near, sunrise or sunset. After an initial period in midwater during the daytime, cod 1 appeared to exhibit a diel pattern of vertical migration, remaining in midwater during the nights of 12/13 and 13/14 June and spending the intervening period on or close to the bottom. The first two ascents and descents (Fig. 2a) occurred during the day. Subsequent movements on and off the bottom at 0330 and 2030 h 13 June and 0315 h 14 June occurred within a few minutes of sunset (2011 h) or sunrise (0334 h), and the final descent also occurred within a few minutes of high-water slack (0323 h). A similar association was apparent for some of the rapid vertical movements during the track of cod 23 (Fig. 2b).

Comparable behaviour occurred at the beginning of the tracks of cod 10 and 20. Both fish initially made vertical movements close to the times of sunset and sunrise (Table 6). Cod 10 went to the bottom during midtide within a few minutes of sunset on the first evening and again the next morning about half an hour after sunrise (Fig. 10a). Cod 20 moved into midwater within 12 min of sunrise on the morning of 31 May and remained there for a period of 1.5 h over the ensuing slackwater (Fig. 10c). Thereafter, the major excursions of both fish were confined almost exclusively to north-going tides. Several of the movements on and off the bottom involved multiple ascents or descents and most occurred within a period extending 60 min either side of the predicted time of local slackwater.

Discussion

Observations of the behaviour of individually identified fish in the open sea are still rare and we are unaware of any similar work on cod with which we can directly compare our results. We therefore discuss them in the context of ideas about the behaviour of cod populations, inferred from echo-sounder records or trawl catches, and results of tracking experiments with individual fish of other species.

Patterns of vertical movement

Three cod exhibited the pattern of vertical migration we have called selective tidal stream transport (Arnold, 1974; Greer Walker *et al.*, 1978) and which in plaice we associate with large-scale spawning migrations (Harden Jones *et al.*, 1979; Arnold and Cook, 1984). These tracks are discussed below. One fish (cod 1) appeared to show a diel pattern of vertical migration, remaining on the bottom during the day and moving into midwater at night; several others exhibited vertical movements at or close to the time of sunset or sunrise. Diel vertical migrations are characteristic of various cod populations in the North Atlantic (Ellis, 1956; Konstantinov, 1958, 1968; Zilanov, 1963; Beamish, 1966) and are often associated with feeding, although the actual pattern may vary widely with season or type of food. Cod eating benthic food, for example, may remain on the bottom at night and move into midwater by day; cod preying on pelagic food may stay on the bottom during the day and move into midwater at night (Brunel, 1972; Turuk, 1973). Further observations are needed to establish the function and importance of diel vertical migrations of cod in the North Sea.

Selective tidal stream transport

Although cod can oppose the current at low speeds, by resting on the bottom on their bellies and the tips of their extended pectoral fins (Harden Jones and Scholes, 1985; Webb, 1989), it is unlikely that they can bury in soft sediments. They must therefore swim to maintain station against the opposing tide, unless they can avoid the main current by positioning themselves in the lee of a sand ridge, or another topographical feature. Such behaviour occurs on Georges Bank in the north-west Atlantic, where 0-group cod (18–20 cm) have been observed lying motionless in troughs between small tidally-induced sand ripples ($h=3$–5 cm, $\lambda=12$–15 cm) (R. G. Lough, pers. comm.). However, we did not see any echoes of sand ridges on the sonar during the tracks of cod 10, 11, and 20 of sufficient size to have provided a lee for cod of 60–70 cm length. We assumed therefore that these fish were swimming against the tide close to the seabed during the south-going stream, cod 10 and 11 moving at the same speed as the tidal current, or slightly slower, and cod 20 about twice as fast.

The differences between the behaviour of these three fish can be explained in terms of swimming performance. For cod of 60–70 cm length the maximum sustained speed is 1–2 L s^{-1} (0.6–1.4 m s^{-1}) (Wardle, 1977; Tytler, 1978). The tidal current would have exceeded this speed close to the seabed for a substantial proportion of each tide during the tracks of cod 10 and 11, causing the fish to lose ground on the opposing tide, or at best hold station, if there were no topographical features to provide a lee. In contrast, cod 20 would have been able to make ground against the current throughout the opposing tide, without exceeding its maximum sustainable swimming speed. At spring tides the tidal current in this area reaches a peak speed of only 0.6 m s^{-1}, compared with 1.4–2.2 m s^{-1} further south in the vicinity of tracks 10 and 11.

Energetic considerations may have also determined the behaviour of fish in midwater. Cod 20 swam downstream with the transporting tide at an estimated speed of 0.5–0.7 L s^{-1}, and thus met Weihs' (1978) criteria for energetically efficient use of the tidal stream. Its behaviour was similar to that of a number of plaice tracked in the same area, which also swam downstream during the transporting tide at a mean speed of 0.6 ± 0.05 L s^{-1} (Metcalfe *et al.*, 1990), and a maturing female plaice which swam downstream for 10 transporting tides at a speed of about 0.9 L s^{-1} (Metcalfe *et al.*, 1992).

Although the vertical movements of cod 10 and 20 were generally quite well synchronized with times of slackwater, those of cod 11 were not. Despite spending only short periods on the bottom, however, the geographical track of this fish still exhibited a clear pattern of selective tidal stream transport, which suggests that, for cod at least, precise synchronization of vertical migration with slackwater is not particularly important in maintaining a consistent direction of transport.

Maintenance of heading

The ability to maintain a heading in midwater for a number of hours on end without visiting the seabed was evident in a number of tracks. Cod 7, for example, deviated by no more than ±45° from the mean heading over an 8-h period. A comparable performance over shorter periods was inferred for yellow and silver eels (Tesch, 1974), plaice (Greer Walker *et al.*, 1978), and Atlantic salmon (Smith *et al.*, 1981). Similar results (Harden Jones, 1981; Harden Jones and Arnold, 1982; Metcalfe *et al.*, 1992) were obtained for plaice fitted with a transponding acoustic compass tag (Pearson and Storeton West, 1987). The ground tracks of a number of other species suggest that the ability to maintain a heading in midwater may be widespread. Consistent courses over periods of 24–48 h, and longer, have been described in bluefin tuna *Thunnus thynnus* (Lawson and Carey, 1972), swordfish *Xiphias gladius* (Carey and Robison, 1981), and blue sharks *Prionace glauca* (Carey and Scharold, 1990), although the sensory basis of this behaviour is not understood. It may be that fish can use the labyrinth for inertial guidance (Harden Jones, 1981, 1984a, b; Sand and Karlsen, 1986), although a recent analysis (Metcalfe *et al.*, 1993) suggests that this is unlikely for plaice. It may be that cod have a magnetic sense (see next section), or possibly a sun compass.

Cues and clues

The variety of behaviour shown during the tracks raises the question of the *cues* or *clues* (Harden Jones, 1984a) to which the fish might have been responding under different conditions. Rhythmic patterns of activity can probably be accounted for by a range of internal or external cues and it is likely that, during selective tidal stream transport, cod synchronize their behaviour with the tides using a biological clock. They may entrain their vertical movements to the 12.5-h cycle of water current reversals as elvers of the American eel (*A. rostrata*) do (McCleave and Wippelhauser, 1987; Wippelhauser and McCleave, 1987, 1988). Cues are, however, an insufficient explanation for the apparently orientated movements seen during many of the tracks and for these it is necessary to postulate the use of one or more external directional clues.

Fish close to a stationary reference point can detect the current by visual or tactile clues and commonly swim against the current. Juvenile cod behave in this way on Georges Bank (Lough *et al.*, 1989), maintaining station by day just above a pebble-gravel bottom. Similar rheotactic behaviour occurred when cod 4–9 went to the seabed and would appear to have been an important component in the orientation of fish that moved away from the coast, as well as for those that showed tidal stream transport. Loss of ground by night, which occurred when cod 10 and 11 were swimming against the opposing tide on the bottom, suggests that visual clues are more important than tactile ones. Positive rheotaxis would account for the downstream heading of cod 20 during the first two transporting tides when the fish left the bottom before the end of the preceding south-going tide. It might also explain the initial difference in behaviour during south-going tides between cod 4 and 7, which swam to the south-east in midwater out of sight of the bottom, and cod 5 and 6, which swam north-east when they were very close to the seabed.

The nature of the clue guiding the fish during their offshore movement is unknown, but there are a number of possibilities. The fish might have taken their heading from some feature of the topography, such as the small sand ridges that run at right angles to the tidal streams, before leaving the bottom (Harden Jones, 1981; Harden Jones and Arnold, 1982). These ridges would, however, only identify the axis of movement and another clue would be required to define the actual direction. One possibility – as appears to be the case in some other teleosts (Walker *et al.*, 1984; Mann *et al.*, 1988; Moore *et al.*, 1990) – is that the cod has a magnetic compass which it uses to determine the direction of its onshore–offshore movements and also to select the direction of the transporting tide. A magnetic compass alone would not enable a migrating fish to determine when to change from one type of behaviour to another and other cues or clues are probably also involved. Sound (Westenberg, 1953) or infrasound (Sand and Karlsen, 1986) generated by wave or tidal action in shallow water near the coast is one possibility, and infrasound is a strong candidate because it propagates long distances in the sea with little attenuation and also produces directional patterns (Karlsen and Sand, 1991). Infrasound has the potential, therefore, to act both as a clue, identifying the direction of the coast, and as a cue, identifying when the fish should switch from offshore movement to selective tidal stream transport.

Two other facets of midwater behaviour are relevant in this context. The gradual turns onto a downtide heading during the tracks of cod 4, 6, and 7 suggest that cod may be able to detect and orientate to the tidal current when they are in midwater, and this in turn raises the question of how they might do so in the absence of the visual and tactile stimuli traditionally associated with rheotactic behaviour (Arnold, 1974). One possibility (Harden Jones and Mitson, 1982) is that fish may be able to detect the noise generated by the tidal current flowing over topographical features on the seabed (Voglis and Cook, 1970). Alternatively, if they were sufficiently sensitive, they might be able to detect the electrical fields generated by tidal currents flowing through the vertical component of the earth's magnetic field (Regnart, 1932; Barber and Longuet-Higgins, 1948; Pals *et al.*, 1982), using the lateral line to determine polarity (Regnart, 1931).

Swimming speeds

The body of the cod is designed for rapid acceleration and high burst speeds (Weihs and Webb, 1983), and sustained swimming is only observed at speeds between 1.4 and 2 L s^{-1} (Videler, 1981). With average midwater speeds of less than 0.9 L s^{-1}, our fish were probably showing the continuous slow acceleration and deceleration observed by Videler at lower speeds in the laboratory. Average cruising speeds of 0.2–2 L s^{-1} have been recorded for plaice (Greer Walker *et al.*, 1978) and European eels (Tesch, 1974); Atlantic salmon have been observed to swim at speeds of 0.2–1.6 L s^{-1} (Smith *et al.*, 1981). The rather slower speeds (0.2–0.9 L s^{-1}) we obtained for cod may be related to the hydrostatic function of the closed swimbladder. A physoclist in neutral buoyancy in midwater has no need to obtain hydrodynamic lift by extending its pectoral fins during swimming, as a negatively buoyant fish does. And partial buoyancy at other depths (Arnold and Greer Walker, 1992) would mean that the fish could obtain hydrodynamic lift at a lower speed than if it were negatively buoyant. The plaice, which lacks a swim-bladder, must swim to stay up at any depth in the water column, as must any physostome such as a salmon, once it leaves the surface and its swimbladder begins to collapse (Blaxter and Tytler, 1978; Ona, 1990).

Migration

The tracks of fish 10, 11, and 20 suggest that selective tidal stream transport may be the mechanism by which the cod population that spawns in the Southern Bight and eastern English Channel migrates to and from its feeding grounds in the central North Sea each year. This hypothesis could be tested experimentally by fishing for migrating cod, as has been done for plaice (Harden Jones *et al.*, 1979; Arnold, 1981; Arnold and Cook, 1984) and sole (Greer Walker and Emerson, 1990), but it remains to be seen if enough cod can be caught in midwater. Unlike plaice, which frequently swim close to the surface during sustained tidal stream transport (Greer Walker *et al.*, 1978; Metcalfe *et al.*, 1992), the track of fish 20 suggests that neutrally buoyant cod may remain in the lower half of the water column. Pre-spawning cod may swim even closer to the bottom because the swimbladder is compressed by the developing gonads. At maturity stage V, for example, the swimbladder of a female cod may be reduced to only 1–2% of body volume (Ona, 1990), insufficient to achieve neutral buoyancy. An alternative approach would be to use electronic data storage tags (Metcalfe *et al.*, 1992) to record the depth of individual fish at frequent intervals over several months and establish patterns of vertical migration in the wild population. This approach would allow fish to be followed through the expected transition in behaviour, which should occur as post-spawning Southern Bight cod move offshore to the deeper water in which they appear to make their main north–south migrations. It would also offer the prospect of carrying out replicated sensory impairment experiments to identify the directional clues used by migrating cod.

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