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Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables II. Reconstruction of plaice ground tracks

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Abstract Between December 1993 and February 1997, 302 electronic data storage tags (DSTs), programmed to record depth at 10-min intervals and temperature daily, were attached to mature female plaice, *Pleuronectes platessa*, and released in the southern North Sea. Fifty tags were returned, 38 of which functioned fully and recorded 2,955 days of data. Twenty-seven tags recorded data over the full period at liberty, and 34 geographical ground tracks were reconstructed. Reconstruction was performed using a two-dimensional tidal stream simulation model that translated vertical movement of fish, recorded by DSTs, into horizontal movement assuming an initial down-tide swimming speed of 0.6 body lengths s^{-1} . Geographical accuracy of reconstructed tracks was assessed based on closeness of fit between (1) reconstruction endpoint and reported recapture position; (2) reconstructed locations and corresponding locations based on tidal data recorded by DSTs using the tidal location method (TLM; location of areas with similar tidal range and time of high water); and (3) DST temperature records and corresponding averaged sea surface temperature data records for corresponding locations. The results demonstrate that the assumptions of the tidal stream simulation model were sufficient to reconstruct geographically accurate representations of the migrations of individual plaice, which have in turn provided new information on the extent, duration, and directionality of movement. Our study demonstrates how DSTs can provide fishery-independent data with direct management applications in behaviourally driven, individual-based predictive models of fish migration.

Introduction

Studies of the behaviour of adult plaice, *Pleuronectes platessa*, have to date focussed mainly on migration in the southern North Sea, where plaice is an important commercial species (Harden Jones 1968; Rijnsdorp and Millner 1996). North Sea plaice-tagging studies date from the early twentieth century (Borley 1916) and have provided scientists with a gross overview of the species distribution (Harden Jones 1968; De Veen 1978; Harding et al. 1978) and have also suggested extensive seasonal migrations (Harden Jones 1968; De Veen 1970, 1978; Rauck 1977). A full interpretation of migration and spatial dynamics has not, however, been possible to date, due to unequal fishing-effort distribution within the North Sea (Hilborn 1990; Rijnsdorp and Pastoors 1995; Jennings et al. 1999; Bolle et al. 2001).

The first applied field studies of plaice behaviour date from the early 1970s, when free-swimming individuals were tagged with acoustic tags and were tracked using sector scanning sonar (Greer Walker et al. 1978; Arnold 1981). These early studies firmly established the link between the fast-flowing tidal stream currents in the southern North Sea and annual pre- and post-spawning migrations. Acoustic tracking, and later, mid-water trawling experiments (Harden Jones et al. 1979; Rijnsdorp et al. 1985; Arnold and Metcalfe 1995), suggested that plaice migration was achieved by the process of selective tidal stream transport (STST, Greer Walker et al. 1978; Harden Jones et al. 1979). This behaviour is characterised by a circa-tidal pattern of vertical movement in phase with the tidal streams. Fish leave the seabed and move into mid-water at about the time of slack water and swim down-tide for the major part of the ensuing north-going or south-going tide. As the tide turns again, the fish return to the seabed where they remain for the duration of the opposing tide.

Egg-survey data have suggested that pre-spawning plaice in the Southern Bight of the North Sea move

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southwards towards the end of the year to spawning grounds located in the Southern Bight and the eastern English Channel (Harding et al. 1978). Egg density distributions have indicated that the fish remain there for 6–8 weeks (Simpson 1959; Cushing 1969, 1990; Harding et al. 1978; Rijnsdorp and Vethaak 1997), before migrating northwards to feeding grounds located on the Indefatigable Banks (Arnold 1981). In support of these findings, Arnold and Metcalfe (1995) used mid-water trawling experiments to demonstrate that during January, spent and maturing plaice could be caught on opposing tides in the Straits of Dover.

The benefit of using selective tidal behaviour resides in the theoretical reduction by up to 40% in the metabolic costs associated with active swimming, if fish swim precisely downstream at their optimal swimming speed (Weihs 1978). Indeed, studies of the orientation of acoustically tagged plaice, although imprecise, have suggested that most migrating plaice do orientate down-tide when swimming (Metcalf et al. 1990, 1993), generally to within $\pm 60^\circ$, and sometimes to within $\pm 35^\circ$ of the mean direction of the tidal stream (Buckley and Arnold 2001). Similarly, average swimming speeds of approximately 0.6 body lengths per second (BL s^{-1}) have consistently been demonstrated (Metcalf et al. 1990; Buckley and Arnold 2001). This is well below the maximum sustainable swimming speed of 1.38 BL s^{-1} (at 10°C) calculated by Priede and Holliday (1980). The maximum observed swimming speed of tracked plaice was 1.4 BL s^{-1} (Metcalf et al. 1990).

In 1995, Arnold and Holford published details of a computer simulation model that predicted the rates and scales of movement of demersal fish on the European continental shelf [originally developed by Arnold and Cook (1984)]. This was essentially a two-dimensional computer simulation model of tidal stream movement that used fish swimming speeds and directions, and the timing and duration of mid-water swimming to predict the movement of individual fish.

In the present study, we used this model to interpret the results from a deployment of 302 plaice tagged with electronic data storage tags (DSTs). Although the use of STST by migrating plaice has been demonstrated, the extent of its use and the full geographical range of migration in the southern North Sea has not. Our aim was to describe the full extent of geographical movement of migrating plaice in the Southern Bight of the North Sea and to test whether the assumptions of STST were sufficient to account for the observed movements of the tagged fish. By assuming STST, we translated vertical movement recorded by the tags into geographical movement, which provided the fundamental reconstruction of fish movement following liberation (Metcalf and Arnold 1997). Although preliminary reports have already indicated the effectiveness of DSTs for describing migratory behaviour (Metcalf and Arnold 1997, 1998; Hunter et al. 2003b, 2003c), this is the first time the full results from this study have been published.

Materials and methods

Data storage tags

The tag employed was a programmable data logger based on the Philips microcontroller (87C552) running at 8 MHz. With a mass data store with 1 Mbit of static RAM (Sony CXK 581000), the tag could store a minimum of 32,000 data samples and retain the information for at least 5 years. The tags were dome-shaped devices (46 mm diameter \times 22 mm maximum height) weighing 55 g in air and 23 g in seawater, designed specifically to be deployed on flatfish (see Fig. 1 in Metcalfe and Arnold 1998). Each tag contained eight analogue sensor channels, two of which were used in the current study. The first recorded depth, derived from pressure using a Keller pressure sensor, from 0 to 100 m (± 0.2 m). The second recorded water temperature from -4°C to 23°C ($\pm 0.03^\circ\text{C}$), using a Fenwall 192-103LET-A01 bead-type thermistor. The tags were encapsulated in opaque, low-density, epoxy resin containing 13% (w/w) microballoons (Robnor PX766C) to minimise total weight. Programming and data retrieval were interfaced using a PC connected to an electronic tag reader. The reader used a two-way serial RS232 infrared optical link to connect to the tags through a clear window in the tags' bases. Power for communication was provided externally by an inductively coupled coil. The tags were

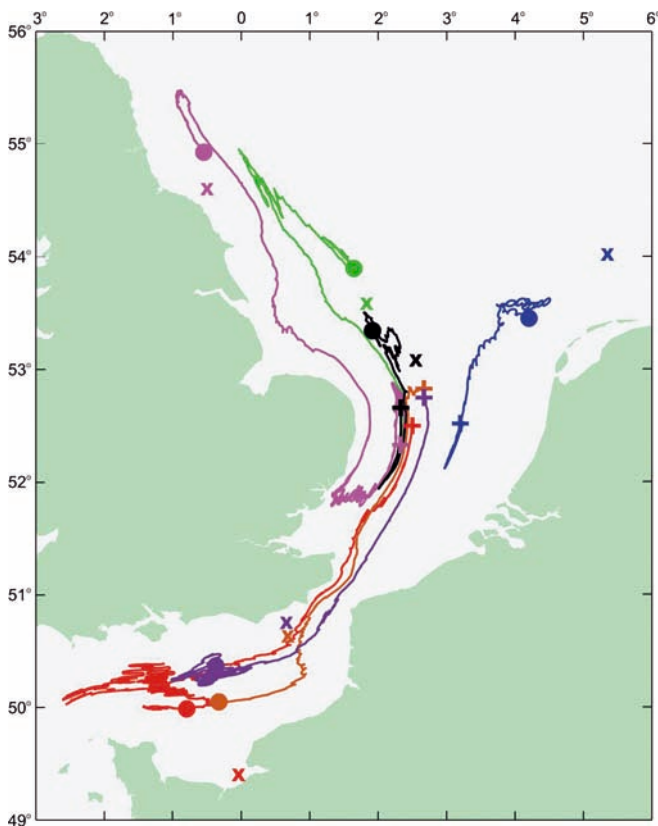


Fig. 1 *Pleuronectes platessa*. Reconstructed ground tracks of plaice tagged with data storage tags (DSTs). The ground tracks shown were reconstructed assuming down-tide swimming at 0.6 BL s^{-1} when fish left the sea bed. The ground tracks illustrate the furthest geographical extent of migration observed during the present study. For release information, see Table 1. Symbols: *Plus sign* Release position; *cross* recapture location; *solid circle* ground-track endpoint. Ground-track reconstructions: *green* DST 1-23; *red* DST 1-28; *pink* DST 1-38; *black* DST 2-81; *brown* DST 4-54; *mauve* DST 5-132; *blue* DST 6-172

programmed to record depth every 10 min and temperature daily (at 00:01 GMT). Using this sampling regime, data could be logged continually for up to 224 days.

Release of tagged fish

The size of the tags made these suitable only for deployment on fish with a minimum total length of 40 cm. Therefore, our experiments did not use male plaice, which rarely attain this size (Rijnsdorp and Ibelings 1989). Mature females were obtained by commercial otter or beam trawl near Smiths Knoll (53°50'N, 02°20'E) in the Southern Bight of the North Sea and returned to Lowestoft to recover in the laboratory aquarium (Scholes 1980). DSTs were attached to the right-hand proximal dorsal surface using two stainless steel wires from standard Petersen disc tags. The plaice were tagged in the aquarium and returned to sea 3–4 days later, in approximately the same area in which they had been caught (Table 1).

The first deployment of 50 DST tagged fish took place on 15 December 1993 in the Southern Bight of the North Sea (Table 1), near Smiths Knoll (Metcalf et al. 1994; Metcalfe and Arnold 1997). Subsequent releases were made in the same area on 18 March 1994 (40 fish), 6 January 1995 (49 fish), 4 December 1996 (109 fish), 18 January 1997 (46 fish), and 3 February 1997 (8 fish). Tags were returned through the commercial fishery following a concerted publicity campaign, and the offer of £25 for each returned tag.

Reconstruction of ground tracks using the tidal stream simulation model

Pressure and temperature data stored in the tag in engineering units were downloaded and converted into depths and temperatures from previously determined calibrations. The depth record was then filtered to generate a time series of vertical movements. Swimming plaice generally climb rapidly into the water column when they leave the seabed (see Fig. 4, Metcalfe and Arnold 1998). A Visual Basic programme extracted sections of the depth record with instantaneous depth changes of > 3 m, which were treated as mid-water excursions. This generated a time series listing times on and off the sea bed.

The time series were then interpreted with the aid of the tidal stream simulation (TSS) model (Arnold and Holford 1995). Based on previous results (Metcalf et al. 1990, 1992; Buckley and Arnold 2001), an initial down-tide swimming speed of 0.6 BL s^{-1} was assumed in addition to STST, when plaice were off the seabed. Therefore geographical movement was computed and not measured directly; however, it was then possible to independently check the overall pattern and extent of geographical movement using the tidal and temperature data recorded by the tag (see below).

The TSS model uses a linear interpolation from tidal stream data tabulated on British Admiralty charts to calculate the tidal stream vector at any specified position (Arnold and Holford 1995). The model estimated speed and direction at any location by completing a triangle based on the locations of the three closest tidal diamonds and interpolating. The interpolations were repeated at half-hourly intervals and a correction was made to allow for the sinusoidal variation of the tidal stream speed through the 14-day cycle of spring and neap tides.

The down-tide swimming speed of 0.6 BL s^{-1} could be increased to an upper limit of 1.4 BL s^{-1} , the maximum speed observed in acoustically tracked tidally transporting fish (Metcalf et al. 1990). Furthermore, the tidal stream model contained no geographical "land"-recognising algorithms, which occasionally led to anomalies for positions where the interpolation of distantly located tidal diamonds drew track reconstructions ashore. The potential for error was greatest in partially enclosed sea areas (e.g. the Thames Estuary), where extensive headlands separate proximal water masses. To prevent these fish moving over geographical "land", it was sometimes necessary to offset the starting position from the

actual release point by a fraction of a degree to obtain a best-fit ground track.

Assessment of ground tracks using tidal data

When tagged fish spent a full tidal cycle resting motionless on the seabed, the sinusoidal rise and fall of the tide was recorded, and it was possible to estimate geographic location using the tidal location method (TLM, see Hunter et al. 2003a for details). This method allows estimation of geographical location based on local time of high water and tidal range (Metcalf and Arnold 1997). Where possible, we calculated geolocation at a number of positions throughout the period at liberty. We attempted to estimate geolocation following all movement events, characterised by days or weeks of extensive vertical excursions. Locations derived using TLM could then be compared with the equivalent positions computed using the TSS model (Arnold and Holford 1995).

Assessment of ground tracks using surface seawater temperature (SST) data

For those dates on which positions generated by the TSS model were compared with geolocations, note was also taken of ambient seawater temperature recorded by the tag. The temperatures at the predicted positions were then compared with SST recorded for the North Sea and eastern English Channel on the same date using averaged SST charts published by the Bundesamt für Seeschifffahrt und Hydrographie (e.g. see Loewe 1998). The tagged fish in this study were released in winter when surface and sea-bed temperature differences in the southern North Sea are minimal due to dynamic mixing (Pingree and Griffiths 1978). By contrast, horizontal temperature differences in winter and spring can be pronounced (e.g. Loewe 1998).

The TLM sometimes generated geographically distant geolocations for fish. This was due to the presence of three North Sea amphidromic systems (Bowden 1983; Hunter et al. 2003a) with which the same combinations of time of high water and tidal range could be associated. Geographically distant positions could normally be discriminated using SST (Metcalf and Arnold 1997). When the SST for a TLM geolocation was more than $\pm 1^\circ\text{C}$ of the temperature recorded by the DST, the position was eliminated from further analysis.

Assessment of ground-track reconstruction accuracy

Assessment of reconstructed fish tracks using tidal and temperature data was not carried out on the basis of geographic precision per se. Rather, we wanted to confirm the prevailing spatial and temporal patterns of movement and direction changes observed in track reconstructions. This approach was sufficient to allow the interpretation of fish movements described in relation to known feeding, transitional, and spawning areas of plaice. An attempt was made to assess the overall geographical accuracy of the STST ground-track reconstruction based on the following three criteria: (1) distance between recapture position (where given) and the computed track endpoint; (2) goodness of fit between STST computed positions and TLM positions generated on the same date(s) based on tidal data recorded by the DST; and (3) goodness of fit between temperatures recorded by tags at the same STST positions used in (2) above, and the average SST values for the same positions on the same dates.

In both categories 2 and 3 above, goodness of fit was assessed using root mean square error (RMSE), where $\text{error}_i = (\text{observed} - \text{induced})_i$. For category 2, error was calculated as geographical distance between TSS and TLM locations. Error for category 3 was the difference between the recorded temperature and the SST temperature for the same location on the same date. It was anticipated that pair-wise comparison of the three categories would

Table 1 *Pleuronectes platessa*. Release, recapture, and ground-track reconstruction details of mature female plaice tagged with electronic data storage tags (DSTs). TRS track running speed; BL body lengths per second; CP catcher position; TLM tidal location method; RMSE root mean square error (see text for details)

Release and recapture									Ground-track reconstruction					
DST	Fish length (cm)	Release position		Recapture date	Recapture position		Days at sea	Days of data	Offset position?	TRS (BL)	CP match range (km)	TLM positions	TLM RMSE	Temp. RMSE
		Lat.	Long.		Lat.	Long.								
Release 1, 15 December 1993 (<i>n</i> = 50)														
1-08	48	52.66	2.33	10/02/94	53.45	2.43	56	56.5	2.66°E	0.73	43.0	5.0	70.2	1.5
1-14	40	52.66	2.33	02/02/94	51.92	2.35	48	0.0						
1-20	40	52.66	2.33	04/01/94	34F2		20	19.9		0.6	51.2	1.0	28.9	0.1
1-21	57	52.5	2.5	13/04/94	–		118	118.1		0.6		10.0	165.3	1.6
1-22	44	52.5	2.5	18/12/93	–		3	2.9						
1-23	42	52.33	2.33	25/08/94	53.58	1.83	252	222.1		0.6	7.42	15.0	66.5	0.5
1-25	40	52.33	2.33	27/03/94	50.85	0.86	102	101.9	2.8°E	0.6	97.2	15.0	139.1	0.8
1-26	42	52.5	2.5	31/01/94	54.8	–0.98	47	47.1		0.6	107.3	4.0	67.0	0.4
1-27	42	52.66	2.33	12/10/94	52.46	3.14	300	112.2		0.6	59.76	4.0	52.0	0.7
1-28	40	52.5	2.5	26/08/94	49.4	–0.04	253	222.1		0.6	59.39	8.0	119.5	0.8
1-30	53	52.33	2.33	17/01/94	50	–0.58	32	32.5	2.66°E	0.6	28.2	4.0	36.3	2.5
1-38	40	52.33	2.33	10/05/94	54.6	–0.5	146	145.9		0.6	41.3	8.0	68.6	1.3
1-48	50	52.5	2.5	15/01/94	50.16	0.4	31	31.3		0.6	36.5	7.0	137.7	0.3
Release 2, 18 March 1994 (<i>n</i> = 40)														
2-70	42	52.66	2.33	24/10/94	–	220	220.1			0.6		16.0	149.3	0.6
2-73	41	52.5	2.5	08/06/94	53.53	1.98	82	81.8		0.6	42.3	5.0	68.4	0.7
2-74	42	52.66	2.33	21/03/94	52.88	2.2	3	3.3						
2-81	44	52.66	2.33	13/07/94	53.08	2.55	116	117.8		0.6	43.6	5.0	132.0	0.4
2-90	44	52.5	2.5	07/04/94	53.16	2	20	20.4		0.6	37.8	1.0	49.9	0.3
Release 3, 6 January 1995 (<i>n</i> = 49)														
3-14	40	52.1	2.66	22/02/95	54.2	3.33	46	0.0						
3-31	46	52	2.33	02/02/95	50.94	0.76	26	0.0						
Release 4, 4 December 1996 (<i>n</i> = 109)														
4-09	40	52.83	2.67	10/12/96	52.83	2.66	5	0.0						
4-114	47	52.83	2.67	17/03/97	53.83	0.83	102	95.2		0.75	87.6	7	68.9	0.7
4-17	50	52.75	2.67	14/12/96	51.92	2.08	10	9.8		0.6	27.4	1	170.3	1.8
4-31	43	52.83	2.67	10/04/97	53.12	2	126	126.0	2.5°E	0.8	57.8	8	96.9	1.4
4-32	42	52.83	2.67	15/12/96	52.75	2.75	10	3.5		0.6		0		
4-38	46	52.75	2.67	05/12/96	52.75	2.75	0	0.0		0.6	259.0	0		2.2
4-39	53	52.83	2.67	31/01/97	50.56	0.58	57	0.0						
4-40	42	52.75	2.67	04/12/96	52.75	2.75	0	0.8						
4-42	41	52.83	2.67	12/12/96	54.1	6	7	6.0						
4-53	40	52.83	2.67	Jan. 1997	50	1	27	32.9		0.6	140.9	1	187.8	1.1
4-54	43	52.83	2.67	10/03/97	50.63	0.68	95	56.9		0.6	96.2	3	79.7	1.6
4-58	44	52.75	2.67	04/03/97	50.83	0.55	89	0.0						
4-63	43	52.75	2.67	26/04/97	52.77	3	142	0.0						
4-76	40	52.83	2.67	05/12/96	52.91	2.62	0	0.6						
4-77	41	52.75	2.67	23/02/97	50.33	0.58	80	0.0						
4-86	40	52.83	2.67	01/12/97	53.96	0.6	361	96.7		0.6	224.7	7	138.2	1.2
4-88	41	52.83	2.67	14/01/97	52.75	1	40	0.0						
4-91	41	52.83	2.67	16/04/97	54.28	0.6	132	47.7		0.6	296.7	0		2.1
4-94	57	52.83	2.67	16/12/96	–		12	11.7		0.6		0		1.8
4-95	52	52.75	2.67	26/09/97	52.83	2.17	295	220.9		0.6	189.7	10	72.0	1.4
Release 5, 18 January 1997 (<i>n</i> = 46)														
5-117	42	52.75	2.67	19/03/97	53.25	2.08	59	50.1		0.6	150.1	4.0	35.1	2.4
5-119	45	52.75	2.67	05/11/97	51.83	2.17	290	0.0						
5-132	50	52.75	2.67	04/06/97	50.75	0.66	136	136.7		0.6	84.2	5.0	101.2	2.2
5-137	40	52.75	2.67	10/02/97	52.5	3.02	22	21.9		0.6	54.6	0.0		0.9
5-143	50	52.75	2.67	02/02/97	50.33	0.51	14	13.7		0.6	12.2	1.0	54.7	0.6
5-150	41	52.75	2.67	no data				67.0		0.6		1.0	7.6	0.6
5-158	40	52.75	2.67	03/03/97	54.2	3.33	43	37.6		0.6	157.3	1.0	40.4	0.3
5-161	40	52.75	2.67	07/09/98	53.1	2.44	596	221.5		0.6	41.8	10.0		1.2
Release 6, 3 February 1997 (<i>n</i> = 8)														
6-168	42	52.52	3.2	06/02/97	52.52	3.15	1	0.0						
6-172	41	52.52	3.2	26/06/97	54.02	5.35	141	142.2		0.6	98.1	3.0	115.9	1.7

allow discrimination of geographically anomalous ground-track reconstructions. All means are presented ± 1 standard deviation (SD).

Results

Tag returns and performance

Fifty tags (16.6%) have been returned to date (November 2003, Table 1) yielding 2,955 days of data. Twenty-seven tags recorded data over the entire period at liberty (1,589 days). Eleven tags stopped recording before recapture (1,366 days), two having reached memory capacity after 222 days, two having failed due to an ingress of sea water around the window in the base of the tag (a manufacturing fault with the third batch of tags), and one having failed to record pressure, probably because of mechanical damage sustained during deployment. The remainder stopped recording due to premature battery failure, a further manufacturing fault with the third batch of tags.

Reconstruction of plaice ground tracks using the TSS model

Thirty-eight tags functioned for some or all of the total period at liberty (Table 1), and geographical ground tracks were reconstructed using the data from 34 of these (Table 1). The 4 remaining records were too short (<48 h) to derive any meaningful track. The full geographical extent of migration suggested by the ground-track reconstructions is shown in Fig. 1.

Twenty-seven of the 34 ground tracks required no further modification to obtain a “best fit” with TLM and temperature data (see below). “Best-fit” reconstructions were obtained for 5 of the 7 remaining ground-tracks by offsetting the release position of the fish and/or increasing the swimming speed. This left just 2 ground tracks for which TLM and temperature data suggested that the TSS ground track did not represent a geographically accurate depiction of the true movements of the tagged fish (see TLM below).

Modified ground tracks

Only four tracks required to be offset from the release position (Table 1, Fig. 2), and swimming speed was increased from 0.6 BL s^{-1} for three ground tracks only (Table 1, Fig. 2), including DST 1-08 (Fig. 2A). The reconstructed tracks of four fish became “trapped” within the Thames Estuary region; however, in each case, the recapture positions demonstrated that the fish did not remain there. These tracks were corrected using minimal offset release positions (Fig. 2). The offset by half a degree of longitude to the east was sufficient to allow alignment between the STST model and tidal data

for DST 1-25 (Fig. 2B) and 1-30 (Fig. 2C), both of which reached the eastern English Channel. DST 4-31 (Fig. 2D) initially moved north to 55° before migrating south into the eastern English Channel for 8 weeks. It then migrated north again, where it was recaptured after 126 days, 55 km from its release position. TLM confirmed that it went north but also suggested that it went further into the eastern English Channel than the STST model predicted. The temperature record, notably at positions C and D (8.5°C and 7.8°C , respectively), also suggested a more easterly position. A best fit of STST reconstruction and TLM locations was obtained by increasing the swimming speed to 0.8 BL s^{-1} and by moving the starting position from 2.67°E to 2.5°E . The fish then returned to the North Sea, ending up very close to the point of release. A similar treatment of DST 1-08 (offset from 2.33°E to 2.66°E and speed increased to 0.73 BL s^{-1} , Fig. 2A) also allowed a better alignment of the final northwards-bearing portion of the track.

The only other track successfully modified to achieve a best-fit reconstruction was DST 4-114 (Fig. 2E). This fish migrated northwards following release. Speeding the track up from 0.6 to 0.75 BL s^{-1} brought the ground-track endpoint and the recapture position into close alignment. The fish reversed direction and moved south before capture, and the faster track allowed close alignment between the latter TLM locations, temperature data, and the recapture position (Fig. 2E).

Assessment of ground-track accuracy—recapture position

Of the 34 ground tracks, 30 were returned with recapture positions (Table 1), only 1 of which was non-specific (the central co-ordinates of the grid-square were used as the recapture location). For 12 of these, there was an interval between the time the tag stopped recording and the time of recapture of between 6 and 375 days (Table 1). When the latter were excluded, the average distance between the end of the STST ground track and the recapture position was $64.6 \pm 55.3 \text{ km}$, and ranged from 12.2 km (5-143 after 14 days at liberty) to 107.3 km (1-26 after 47 days at liberty; Table 1). For tags that stopped recording prior to recapture the distance between ground-track endpoints and recapture positions ranged from 7.4 km (1-23 recorded 222 of 252 days at sea) to 296.7 km (4-91 recorded 48 of 132 days at sea). Tag 4-42 had a discrepancy of 259 km after recording 6 of 7 days at sea (Table 1). This was assumed to be a reporting error.

Assessment of ground-track accuracy—tidal location method

A minimum of one tidal sine wave suitable for estimating geoposition using TLM was located in all but

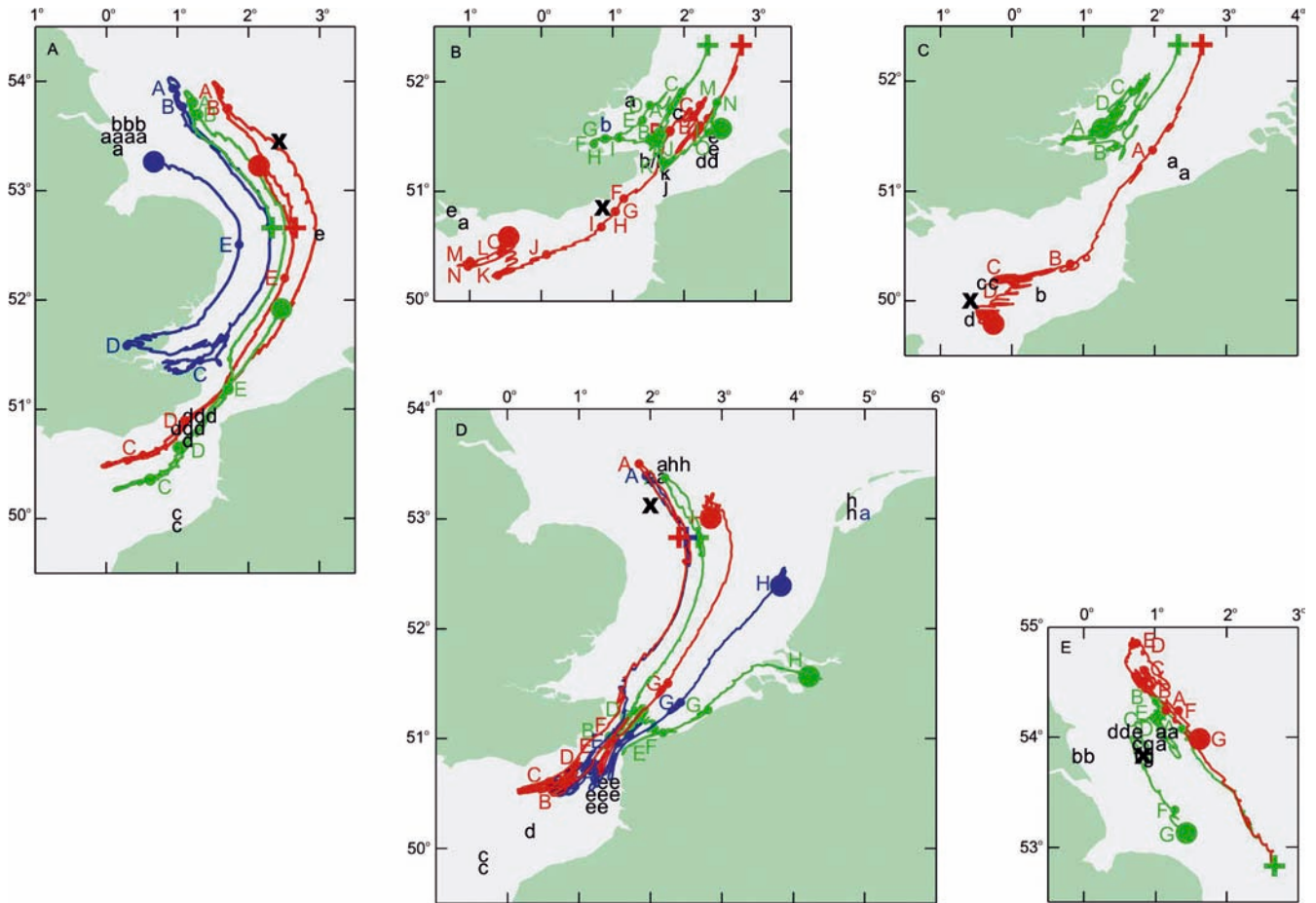


Fig. 2A–E *P. platessa*. Reconstructed ground tracks of DST tagged plaice. Ground tracks initially reconstructed assuming down-tide swimming at 0.6 BL s^{-1} , then either offset from the release position and/or speeded up to achieve better alignment between the ground-track, the tidal location method (TLM) positions, and recapture location. Original reconstructions are in *green*; intermediate reconstructions (where relevant) are in *blue*; final reconstructions are in *red*. Lowercase lettering indicates sequential geolocations made using TLM (see text). Blue lettering indicates geolocations subsequently eliminated using surface seawater temperature (SST) data. Corresponding locations on the ground track [calculated using the tidal stream simulation (TSS) model] shown in *uppercase lettering*. Symbols: *Plus sign*

release position; *cross* recapture location; *solid circle* ground-track endpoint. **A** DST 1-08. The original ground track (*green*) terminated $>1.5^\circ\text{S}$ of the recapture location. Starting location was speeded up to 0.73 BL s^{-1} (*blue*), then offset 0.33° to the east (to 2.66°E , *red*). **B** DST 1-25. The original ground track (*green*) became trapped in the outer Thames Estuary region. Release position offset from 2.33°E to 2.66°E (*red*). **C** DST 1-30. As for **B** above. **D** DST 4-31. The original ground track did not pass into the eastern English Channel (*green*). Release position was offset from 2.67°E to 2.5°E (*blue*), and swimming speed increased from 0.6 BL s^{-1} to 0.8 BL s^{-1} (*green*). **E** DST 4-114. Swimming speed increased from 0.6 BL s^{-1} (*green*) to 0.75 BL s^{-1} (*red*)

five ground tracks (Table 1). The average number of tidal sine waves measured per track was 5.6 ± 2.1 . The TLM located geopositions for 5.0 ± 1.6 of these sine waves and generated an average output of 25.5 ± 8.6 geopositions per ground track. Average RMSE for TLM was $90.0 \pm 48 \text{ km}$. Four short tracks of 22 days or less were the only tags from which no tidal data could be derived (Table 1). For example, DST 4-94 exhibited vertical activity in phase with south-flowing tides throughout 11 days at liberty; therefore tidal parameters could not be calculated.

The TSS model placed both DST 1-21 and 4-53 further north than TLM, and for DST 4-53, further north than the recapture position (Fig. 3). Neither offsetting the release position nor altering the swim-

ming speed generated tracks for either fish that passed into the English Channel. By moving the release position of DST 1-21 inshore from 2.5°E to 2°E it was possible to correct the initial portion of the track, but the reconstructed track then became “trapped” in the Thames Estuary.

The ground track for DST 2-70 (Fig. 4) suggested a slow northwards progression following release over approximately half a degree of latitude. The TLM, however, indicated an anti-clockwise migration around Southern Bight. This was the only instance in the present study where the movement pattern observed from tidal data could clearly not be accounted for using the assumptions of the TSS model (Arnold and Holford 1995).

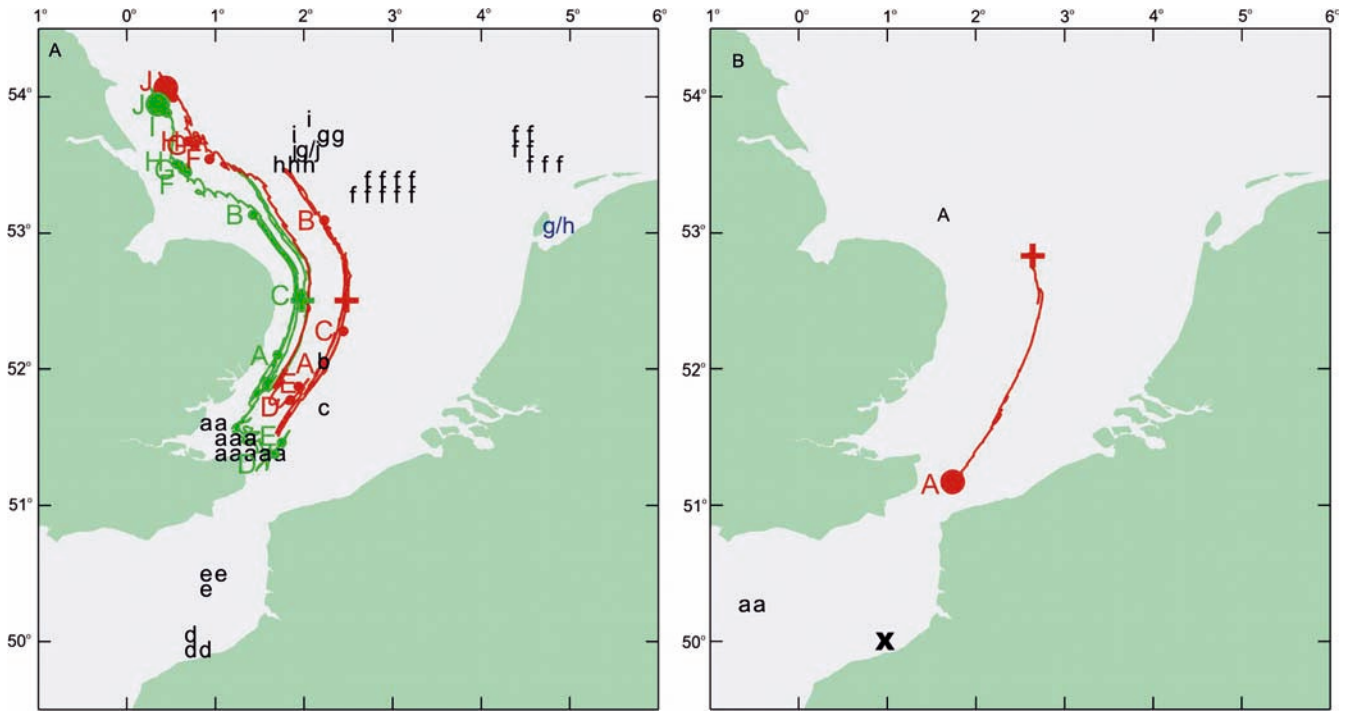


Fig. 3A, B *P. platessa*. Ground-track reconstructions for DST-tagged plaice that demonstrate poor alignment with TLM and recapture locations. For symbols and annotation, see Fig. 2. **A** DST 1-21. Original ground track (green) offset from 2.5°E to 2°E (red). **B** DST 4-53

Assessment of ground-track accuracy—sea surface temperature

Comparison of DST recorded temperature with SST at corresponding geolocations generated by TLM allowed the elimination of 17.3% of potential geolocations. However, temperature differences were unable to

eliminate alternative geolocations in all cases (Fig. 4, Fig. 5). The RMSE values comparing the discrepancy between recorded temperatures and the computed STST locations corresponding to the TLM geolocations above suggested that on average the difference between recorded temperature and SST was $1.1 \pm 0.7^\circ\text{C}$ (Table 1).

Confirmation of geographical accuracy of ground tracks

None of the assessment criteria (recapture position, TLM and temperature RMSE) was on its own sufficient for the validation of individual reconstructions (Table 1). Discrepancies between tracks (e.g. no recapture position or date provided, lack of tidal data) often prevented the full validation of ground tracks and meant that the pairwise comparisons of the assessment criteria (Fig. 6) were of limited value. These did illustrate the tendency of a small number of tracks to score consistently low (e.g. DST 1-20), and consistently high (e.g. DST 4-53) RMSE values (Table 1). Most tracks, however, exhibited relatively low RMSE values, suggesting that the majority of ground tracks gave a realistic representation of the geographical movement of the fish.

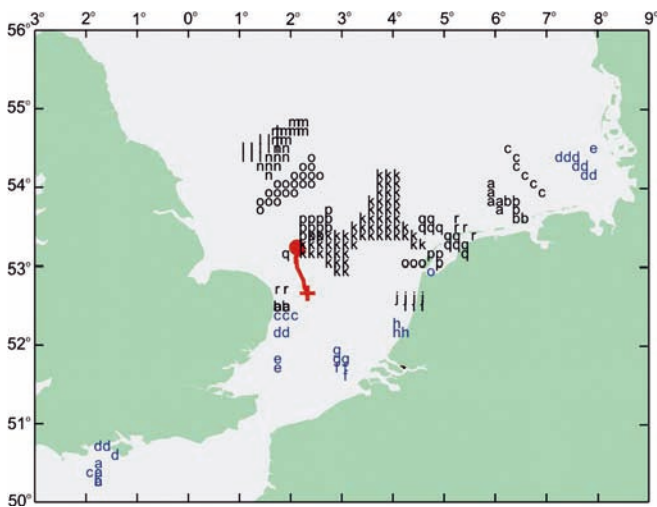


Fig. 4 *P. platessa*. DST 2-70. For symbols and annotation, see Fig. 2

Migration patterns of DST-tagged plaice suggested by reconstructed ground tracks

Distance and direction of movement by DST-tagged plaice is plotted monthly in Fig. 7. Migration principally followed a north–south axis. Movement was most

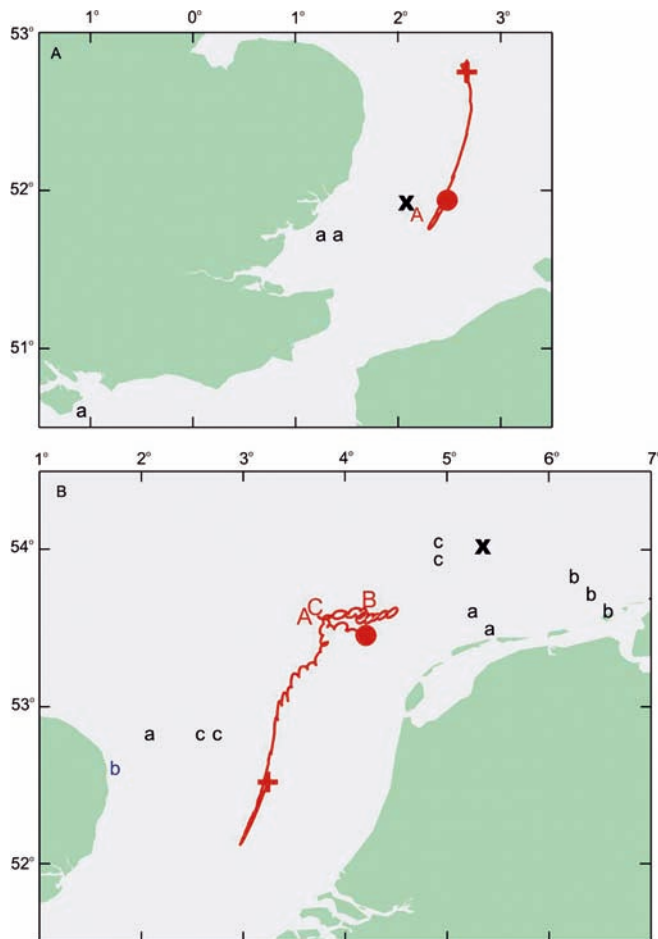


Fig. 5A, B *P. platessa*. Ground-track reconstructions for DST-tagged plaice with high RMSE values for TLM and temperature, due to inability to eliminate distant TLM locations based on SST criteria (see Materials and methods). **A** DST 4-17. **B** DST 6-172

pronounced between December and February, with little movement occurring from the end of April onwards. With the exception of DST 6-172 (Fig. 5), which migrated along the north coast of Holland, the other fish remained on the west of the North Sea in the tidal stream that runs parallel to the U.K. coastline (Fig. 1, Fig. 7). Fourteen ground tracks exhibited relatively large-scale geographical movement ($>2.0^\circ$ latitude, approximately), and only one individual at liberty for more than 1 week demonstrated no obvious migration (DST 5-161).

Plaice released in December (releases 1 and 4, Table 1) initially moved north (7 fish), south (12 fish), or not at all (DST 4-42, 6 days at liberty). Only 2 of the northbound fish maintained the northerly bearing, DST1-26 (recaptured 31 January 1994) and DST 4-95 (recaptured 26 September 1997), while the others reversed direction by the end of December, except for DST 1-23, which did not start moving south until 29 January 1994. All 8 fish released in January (release 5, Table 1) moved south following release. Of the fish released in March (release 2, Table 1), 2 fish moved northwards,

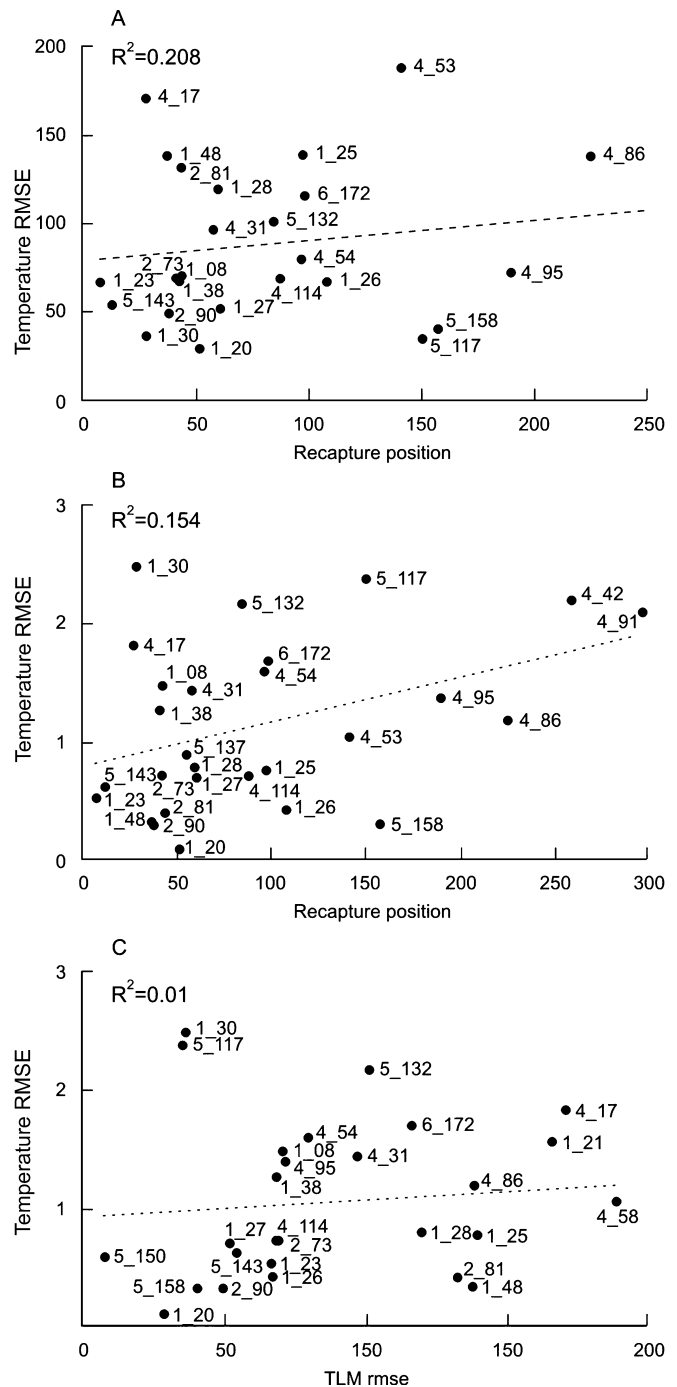


Fig. 6A–C *P. platessa*. Pair-wise comparison of recapture location, TLM and temperature RMSE (see Materials and methods). Labels shown are tag numbers. **A** Recapture position versus TLM. **B** Recapture position versus temperature. **C** TLM versus temperature

and the 1 southerly bearing fish reversed direction after several days.

In total 11 ground tracks (32%) indicated southwards migration into the eastern English Channel (south of 51°N): 8 fish were recaptured there. Before the end of December, DST 4-94, (week 50), 4-31 (week 51), 1-30,

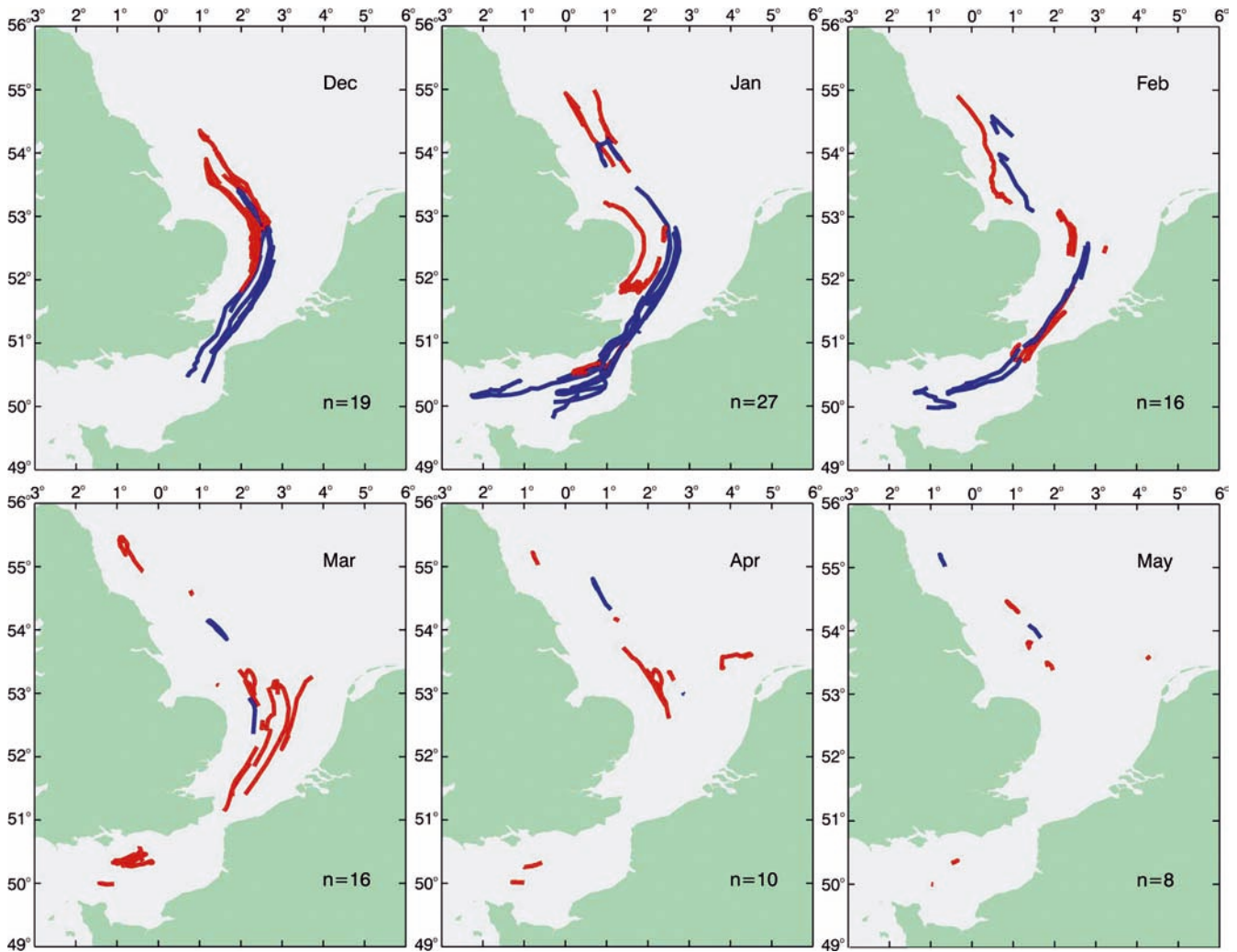


Fig. 7 *P. platessa*. Monthly composite plots of reconstructed plaice ground tracks. Blue Southwards migration; red northwards migration

and 1-28 (week 52) had passed through the Dover Strait. The number of fish in the Channel peaked at 38% (week 2) then declined to 23% (week 9) and remained constant thereafter. This was due to DST 1-25, 1-28, and 5-132, which remained in the Channel until recapture on 27 March 1994, 26 August 1994, and 04 June 1997, respectively (Table 1). A further 3 ground tracks demonstrated northwards migration following visits to the eastern English Channel. DST 1-08, 4-31, and 4-86 entered the Channel between 24 December and 22 January, and returned between 3 February and 27 February, having spent 21, 42, and 37 days, respectively, below 51°N.

Between January and March, the number of fish located between 51°N and 53°N varied between 58% (week 3) and 29% (week 7). By the end of March, the majority of plaice were moving northwards, and a steep decline in the number of plaice between 51°N and 53°N was observed. From 50% in week 12, this dropped to zero fish by week 15, and following which

no further plaice were observed in Southern Bight. By week 22, data were available for five tags only.

Discussion

Geographical accuracy of ground tracks

Three independent but complimentary approaches have been employed to successfully determine the extent of geographical movement of free-ranging demersal fish. The first and principal method involved the use of a computer TSS model to calculate tidal transport of fish during periods of activity when fish are off the seabed (Arnold and Cook 1984; Arnold and Holford 1995). DST 1-21 (Fig. 5) was the only fish that suggested that the TSS model may sometimes be unable to reconstruct ground tracks in tidally complex areas. The second method used tidal data (tidal range, times of high and low water) recorded when the fish remained stationary on the seabed over the duration of one or more tidal cycles (Metcalf and Arnold 1997; Hunter et al. 2003a). The TLM is already known to produce geolocations with an accuracy to within 40 km over much of the

Southern Bight (Hunter et al. 2003a). The third method involved the comparison of DST-recorded seawater temperature with synoptic charts of sea surface temperature (Metcalf and Arnold 1997, 1998).

Elimination of all geographically distant geolocations using SST data (Fig. 4, Fig. 5) could have improved overall accuracy even further. Indeed, the relatively large confidence intervals suggested by the temperature RMSE ($1.1 \pm 0.7^\circ\text{C}$) indicate that SST is the least accurate of the validation procedures. The relatively low definition SST data could possibly be improved upon using cloud-corrected advanced very high resolution radiometer data, such as has recently been applied to describing the large-scale movements of Atlantic Ocean green turtles (Hays et al. 2001).

Absence of any of the assessment criteria was not in itself grounds for rejecting the general pattern of a ground track. Discrepancy between the computed TSS ground-track endpoint and reported recapture clearly indicated an incorrect reported recapture location for one individual only (4-42, Table 1). Large discrepancies could be accounted for in another three fish by the long intervals between the time the tag stopped recording and the time of recapture (4-86, 4-91, and 4-95). The same was true after relatively short time intervals for a further two fish showing active STST (5-117 and 5-158). Previous studies using acoustic telemetry have demonstrated that actively migrating plaice can move up to 20 km per day (Metcalf et al. 1990).

Although we have not determined absolute measures of geographical precision, the general correspondence between the three methods described suggests that the ground tracks produced good descriptions of the timing, extent, and directionality of plaice migration. The addition of extra sensors to DSTs may allow additional validation procedures in future studies, for example, using light-based geolocation (Welch and Eveson 1999; Metcalf 2001).

Validity of the tidal stream simulation model

Twenty-nine (85%) of the ground tracks presented were satisfactorily reconstructed using a swimming speed of 0.6 BL s^{-1} (Metcalf et al. 1990; Buckley and Arnold 2001). Five remaining tracks required either minimal offset of the starting location or an increase in the swimming speed to allow better alignment between the ground-track reconstruction and the validation criteria. The maximum swimming speed required to achieve alignment was 0.8 BL s^{-1} (Table 1), well below the maximum observed swimming speed (1.4 BL s^{-1}) of acoustically tracked fish (Metcalf et al. 1990). Furthermore, we found only one fish in the present study for which the ground track could not reasonably be reconstructed from the record of vertical movement and the TSS model (DST 2-70, Fig. 5).

These results provide strong evidence, therefore, that the migration of plaice in the southern North Sea can be

accounted for by the simple assumption that fish swim directly down-tide with an approximate swimming speed of 0.6 BL s^{-1} . These results confirm previous observations of the use of STST by plaice migrating in the southern North Sea (De Veen 1978; Greer Walker et al. 1978; Harden Jones et al. 1979; Arnold 1981; Arnold and Metcalf 1995; Metcalf and Arnold 1997). Further alterations to the starting parameters of the model, or even the use of intermediate starting positions in the case of tracks that become trapped in the Thames Estuary, would doubtless allow the generation of more geographically precise ground tracks. However, the minimal level of adjustment required and the accuracy of the ground tracks generated emphasises the robustness of the TSS model (Arnold and Cook 1984; Arnold and Holford 1995) in describing migration within the population studied.

Migration patterns of plaice in the southern North Sea

The ground-track reconstructions presented here provide important new information with regard to the extent, duration, and directionality of plaice migration in the southern North Sea. Our results illustrate a predominantly southwards migration following release in December and January, into both Southern Bight and the eastern English Channel. There were only two individuals from the current study that migrated northwards following release and that were conceivably following a pre-spawning migration. Although we are unable to determine whether this is the case, a spawning ground off the coast of Flamborough is well established (Harding et al. 1978; Heesen and Rijnsdorp 1989).

We also found that a third of the tagged fish visited the eastern English Channel, a figure significantly higher than has been predicted by conventional tagging studies (Bolle et al. 2001). Given that nine tags were recaptured within the first 30 days of release, it seems reasonable to speculate that the number of fish passing through the Dover Strait may actually be higher. Egg survey data have already been used to calculate residence times of plaice on spawning grounds in the eastern English Channel at approximately 6 weeks, a figure largely confirmed by our observations; however, our results also indicate that of the 11 fish that visited the eastern English Channel, at least 2 fish (18%) remained there following the close of the spawning season. Both this and the previous observation have important fisheries management implications. North Sea and English Channel plaice are currently managed as distinct stocks, between which mixing is assumed not to occur (Anonymous 2002). Recent studies examining Atlantic tuna stocks have shown that different mixing rates can yield grossly different predictions of abundance trends (Porch et al. 1995).

Furthermore, our work reveals that as well as being an important spawning area (Cushing 1969, 1990; Harding et al. 1978), Southern Bight is also effectively a

transitional area, with none of the plaice studied remaining in the area between 51° and 53°N by the end of April. Although only five tags recorded beyond the close of May, the horizontal movement undertaken by plaice by the end of April onwards was already minimal, suggesting that the fish were already located on their summer feeding grounds, distributed between 53° and 55°N.

Relevance of results and future applications

The purpose of this study was not to provide details of how the exact daily location and behaviour patterns of individual fish could be exhaustively checked from archived records of depth and temperature. Rather, our results show how, by using electronic data loggers to record simple behavioural and environmental data, it was possible to use a simple two-dimensional model of the tidal streams to reconstruct geographically realistic movements of fish on the European continental shelf over time periods sufficient to describe complete spawning migrations.

This data, therefore, is highly applicable to the construction of biologically based predictive models of the spatial dynamics of North Sea flatfish populations (Metcalf et al. 1999). Since European common fisheries policy increasingly employs the use of marine protected areas in quota management (European Commission 2001), it is essential that such management options are underpinned by a thorough understanding of the spatial and temporal dynamics of the managed species (Horwood et al. 1998; Metcalf et al. 1999). Track reconstruction provides a fundamental method by which accurate predictions can be made with regard to the occupancy and transition times of fish in defined areas.

Specifically, the implementation of marine protected areas in the North Sea as a conservation measure (European Commission 2001) will be successful only if the protected areas take account of the seasonal movements and spatial distribution of the fish to be protected. We anticipate, therefore, that the incorporation of DST data into a behaviour-driven individual-based model of plaice migration in the North Sea (Metcalf et al. 1999) may have an important future role to play in North Sea stock recovery plans.

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