Migration route and spawning area fidelity by North Sea plaice

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Data from plaice, *Pleuronectes platessa* L., tagged with electronic data storage tags, were used to test whether these fishes exhibited migration route and spawning area fidelity in successive spawning seasons. Depth and temperature data were recorded for each fish over 365–512 days in the central North Sea and this information was used to reconstruct movements based on tidal locations. We discovered highly directed seasonal migrations from the winter spawning area south of a major topographical feature, Dogger Bank Tail End, to summer feeding grounds 250 km to the north in deep, cold, thermally stratified water. Our results show synchronous timing of migration, repeated pre- and post-spawning migration routes and 100% spawning area fidelity, including two individuals that returned to within 20 km of their previous season's spawning location. This is the first study to provide a complete reconstruction of annual migrations by individual fishes, showing strong homing behaviour along consistent migration routes.

Keywords: *Pleuronectes platessa*; electronic data storage tag; behaviour; homing; philopatry; metapopulation

1. INTRODUCTION

Concern about unsustainable levels of exploitation and poor recovery of many fish stocks has stimulated interest in the population structure and spatial dynamics of commercially exploited species (Rose 1993; Stephenson 1999; Hutchings 2000; Reynolds *et al.* 2002). We now know that traditionally recognized fish 'stocks' often possess metapopulation structure (Hanski & Gilpin 1997), composed of subpopulations or spawning components with various levels of exchange depending on the degree of spatial and temporal overlap (Smedbol & Stephenson 2001). Therefore, effective conservation of fish stocks requires a thorough understanding of the movements of individuals (Stephenson 1999; Metcalfe *et al.* 2002).

It is extremely difficult to make frequent, repeated observations necessary to describe marine fish spatial dynamics. This has meant that, to date, inferences have been made from observations of egg (e.g. Harding *et al.* 1978) and fish (e.g. Hutchings *et al.* 1993) densities, tagging experiments (e.g. Lear 1984; Taggart *et al.* 1994; Bolle *et al.* 2001) and genetic studies (e.g. Ruzzante *et al.* 2000; Hutchinson *et al.* 2001; Horau *et al.* 2002). These techniques have provided important insights, but they do not describe the demographic components of population structure (Horau *et al.* 2002), such as natal homing, fidelity to migration routes and spawning sites. This information is important for effective conservation (Stephenson 1999).

Recent technological advances now offer a variety of sophisticated methods for studying the real-time movements of marine fishes in their natural environment (Sibert & Nielsen 2001; Robichaud & Rose 2001; Thorrold *et al.* 2001). The use of computerized tagging in parti-cular now allows access to behavioural information from bottom-dwelling fishes, which tend to be highly mobile (Metcalfe *et al.* 2002), and which are vulnerable to overexploitation (Hutchings 2000; Pauly *et al.* 2002). While homing to spawning grounds has long been recognized in diadromous fishes (Metcalfe *et al.* 2002), this has only recently been indicated in a marine broadcast spawner, the Atlantic cod, *Gadus morhua* L. (Robichaud & Rose 2001). However, we know little about migration patterns and behaviour outside of the spawning season.

Here, we report on the first study of complete annual migration cycles for individual bottom-dwelling fishes. We gathered detailed information on the behaviour of individual plaice, *Pleuronectes platessa* (L.), over periods of 1 year or more. Plaice is the principal flatfish exploited from the North Sea, where it is managed as a single stock and is being exploited outside safe biological limits (Anonymous 2002). Although plaice have been the subject of intense study over the past 100 years, the population substructure has only recently been revealed as a result of experiments using electronic data storage tags (Hunter *et al.* 2003*b*). These fish typically reach maturity at 2–3 years of age (Rijnsdorp 1993), and then make annual migrations to their winter spawning grounds, often using tidal streams to assist with navigation and transport (Harding *et al.* 1978; Metcalfe *et al.* 2002).

We used electronic data storage tags to study the behaviour of individual plaice in the central North Sea. With data series covering two successive spawning seasons, we posed the following questions fundamental to the demography of this 'stock'. First, do individuals use the same spawning areas in successive years? Second, do individuals use the same migration routes in successive years? The results describe the timing and extent of migration with a level of accuracy that has not previously been possible, providing a behavioural underpinning to spatial dynamics that has implications for fish stock conservation.

Table 1. Release, recapture and ground-track reconstruction details of mature female plaice carrying electronic data storage tags.
(Grid references for latitude (°N) and longitude (°E) are presented in decimal degrees. Abbreviations: DBTE, Dogger Bank Tail End.)

plaice		1	2	3	4	5	6	7
release length of fish (cm)		43.0	38.0	40.0	43.0	38.0	43.0	39.0
release position	latitude	55.9	55.9	55.9	56.0	56.0	55.9	56.0
	longitude	4.2	4.3	4.3	4.3	4.2	4.3	4.4
recapture position	latitude	56.5	55.5	56.6	55.8	54.8	55.8	56.0
	longitude	3.0	5.5	4.1	4.7	4.5	4.7	6.3
number of geolocations		15	17	21	20	14	14	18
final geolocation	latitude	56.5	56.2	55.2	54.9	55.1	55.5	55.2
	longitude	3.6	4.9	4.7	6.1	4.9	4.8	5.3
final geolocation date		28/4/94	23/11/98	7/12/98	21/11/99	31/12/98	18/11/98	30/1/99
reported capture date		7/5/99	16/12/98	1/7/99	3/3/99	20/1/99	3/3/99	23/2/99
date of last data		1/5/99	5/12/98	26/12/98	23/1/99	7/1/99	6/1/99	2/2/99
difference (km)		35.8	89.9	160.9	125.0	38.6	30.3	114.9
battery fail? (Y/N)		N	N	Y	Y	N	Y	N
recorded days of data		512	365	386	414	398	397	424
total distance travelled (km)		870	1247	1922	1388	1069	566	1443
migration schedule:								
spawning area		10/01/98	27/12/97		03/01/98		13/01/98	22/01/98
DBTE (post-spawning)		02/02/98	19/02/98		20/02/98		03/03/98	24/04/98
feeding area		13/02/98	05/03/98	01/02/98	08/03/98	20/01/98	13/03/98	
thermocline in (pre-spawning)		25/10/98	25/10/98	25/10/98	25/10/98	24/10/98	11/10/98	06/10/98
thermocline out (pre-spawning)		28/10/98	29/10/98	30/10/98	31/10/98	26/10/98	17/10/98	10/10/98
DBTE (pre-spawning)		19/11/98	19/11/98	15/11/98	16/11/98	26/10/98	27/10/98	
spawning area		27/12/98			20/12/98	24/11/98		20/01/99
DBTE (post-spawning)		10/02/99						
feeding area		19/02/99						

2. MATERIAL AND METHODS

(a) *Capture and tagging*

The plaice described were returned from a release of 117 mature females (minimum size 35 cm total length), tagged with Lotek LTD-1200 electronic data storage tags (Lotek, Ontario, Canada). The tags weigh 2 g in water (16 g in air), and were programmed to record temperature and depth (pressure) every 10 min. The maximum duration of battery life was approximately 18 months. The tags were designed to retain stored data for up to 25 years, and were returned via the commercial fishery.

Capture, tagging and release were undertaken from a commercial trawling vessel on 5–6 December 1997 (table 1). Trawl durations were *ca.* 30 min using a 90 mm trawl mesh. Following capture, plaice were transferred to a 20 l holding tank on the ship. After 15 min, the data storage tags were attached dorsally with stainless steel wire and secured on the ventral surface by a single 25 mm plastic (Petersen) disc, which protected the fishes' skin. The tagged fish were released when the vessel had come to a standstill.

(b) *Data interpretation*

Raw data were converted into depth and temperature using previously determined calibrations. We assumed that depth transitions of greater than or equal to 3 m between successive measurements indicated transition from on-bottom to midwater swimming activity (Priede & Holliday 1980). The depth record was filtered to generate a time-series of vertical movements and seabed depths (Arnold & Holford 1995). Seabed depth and temperature were averaged daily.

The position of each fish from release to recapture was described using the tidal location method (Hunter *et al.* 2003*a*). This method estimates geographical location based on the time of high water and tidal range, measured by the depth (pressure) sensor when a fish remains motionless on the seabed over a full tidal cycle (or longer). We aimed to use the method with a minimum interval of two weeks from October to May, and at monthly intervals during the summer. We attempted to estimate position following all movement events, characterized by days or weeks of extensive vertical excursions. A geolocation-based ground-track was then created by fitting a piecewise linear curve through the resulting geopositions.

3. RESULTS

To date (January 2003), 46 data storage tags have been returned to us (39%). Details are given in table 1 for the seven fish for which we have records over a full annual cycle. Inspection of early results revealed that Dogger Bank Tail End was a key topographical feature in the observed migrations. This is the northeasterly projection of Dogger Bank, a ridge running northeasterly along the central North Sea, rising to as little as 20 m depth.

(a) *Physical data recorded by the tags*

The average daily depth, temperature and number of hours that the fishes spent swimming in mid-water are shown in figure 1. Depth records (figure 1*a*) indicate a transition from relatively shallow water (less than 50 m) in the two months following release into deeper water (greater than 60 m) during the spawning season between February and March, where they remained until September. Between October and December, the plaice moved back into shallow water.
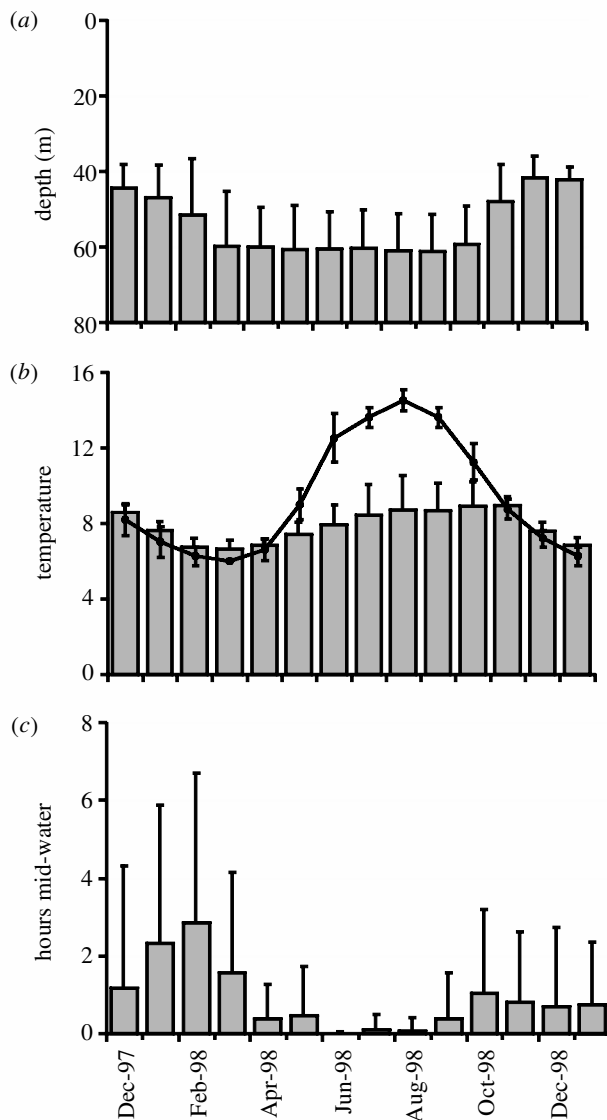

Figure 1. Average monthly depth, temperature and hours spent swimming in mid-water (± s.e.) recorded by seven plaice tagged with electronic data storage tags, which recorded data over a year or more. (*a*) Mean monthly seabed depth. (*b*) Mean monthly ambient temperature (histogram) in degrees and averaged sea surface temperature at 56° N, 4.3° E (line plot), in °C. (*c*) Mean number of hours spent each month swimming above the seabed.

The plaice remained below 9 °C throughout the summer, significantly below the average sea surface temperature (figure 1*b*). This confirmed a deep, cold, thermally stratified location north of the thermal front (Pingree & Griffiths 1978). Swimming activity was greatest between January and March and peaked during the spawning season in February (2.9 ± 3.6 h per day; figure 1*c*). Individual fish rarely spent more than 4 h in mid-water per day. Fish swam infrequently during the feeding season between April and September, but were increasingly active from October onwards.

(b) *Patterns of migration*

Pairwise comparisons of depth and temperature showed that five of the fish had similar movements and behaviour. This was confirmed by geolocation. We will therefore follow the individual shown in figure 2*a* in detail, to help
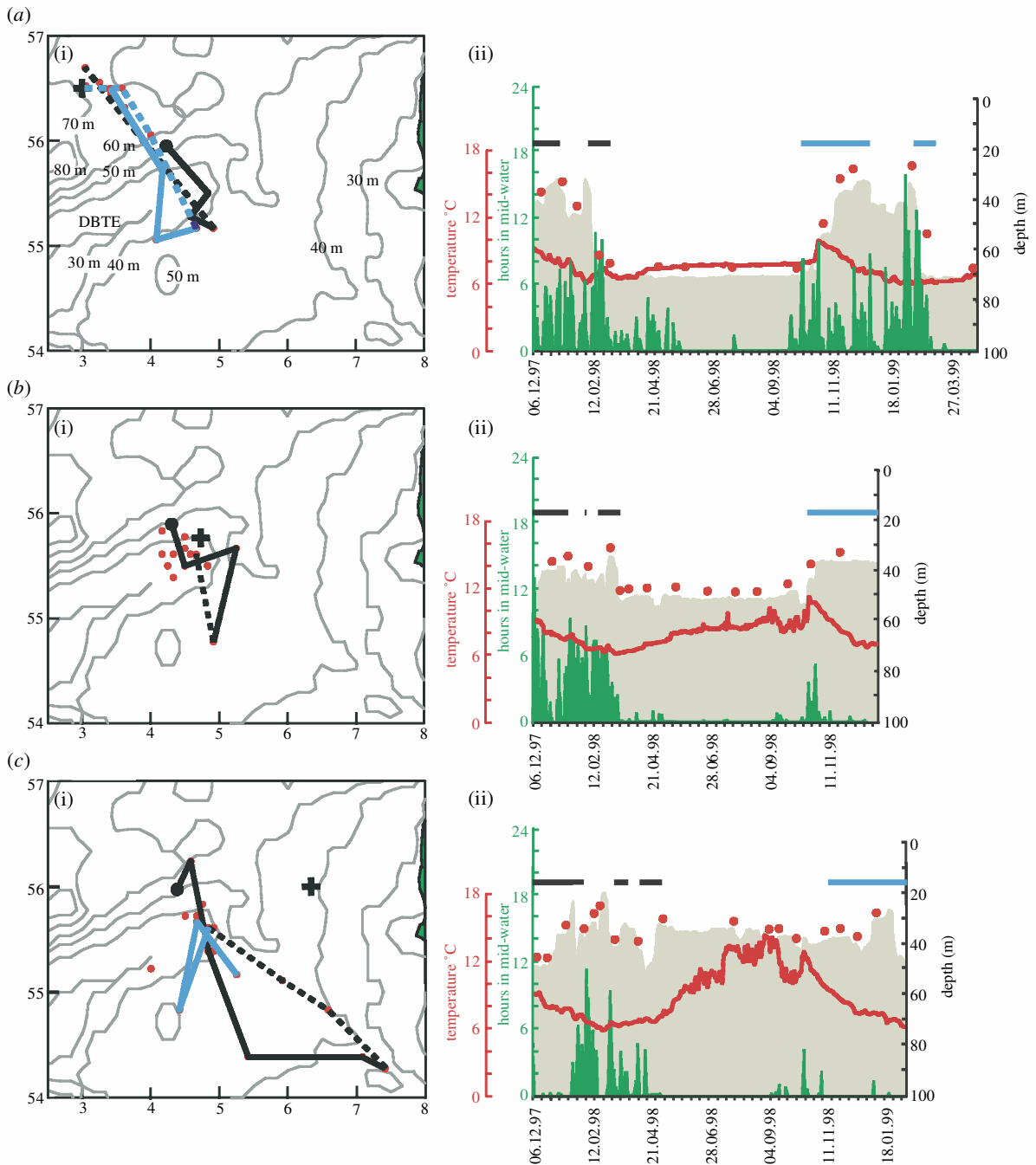
Figure 2. Ground-track reconstructions and depth, temperature and activity plots for three plaice ((*a*) plaice 1; (*b*) plaice 6; (*c*) plaice 7) tagged with electronic data storage tags, which recorded data over a year or more. See text for a detailed interpretation of figure 1*a*. Key: solid lines, pre-spawning migration; broken lines, post-spawning migration; black lines, 1997–1998; blue lines, 1998–1999; grey lines, depth contours; large black circle, release position; cross, recapture location; red circles, individual geolocations; DBTE, Dogger Bank Tail End. Grey shaded area, average daily seabed depth; red line, temperature; green shaded area, average number of hours spent in mid-water per day.

interpret the data (see also table 1). Figure 2*a*(i) shows the release position of the fish (black circle), followed by a southerly movement (solid black line) to a known spawning area (see Harding *et al.* 1978). Depth, temperature and swimming activity for this segment of its annual cycle are shown in figure 2*a*(ii), under the black bar. Here, we see the fish moving up and over the bank (grey peak), which it crossed in 36 days. The green spikes show corresponding swimming activity and the red line shows decreasing winter water temperature. The fish then spent 23 days on the spawning area before heading northward,

re-crossing the bank in only 11 days as part of a 27-day, 205 km long migration to the northwest (figure 2*a*(i), broken black line). This movement corresponds to the second peak in depth shown in figure 2*a*(ii) followed by a rapid drop to lower depths. The fish remained on this northern feeding area for 251 days until 7 October 1998. This period was characterized by minimal change in temperature or depth and low swimming activity, shown by the long straight depth and temperature profile in figure 2*a*(ii). During the second migration season the fish became active in early October and its trip back over the
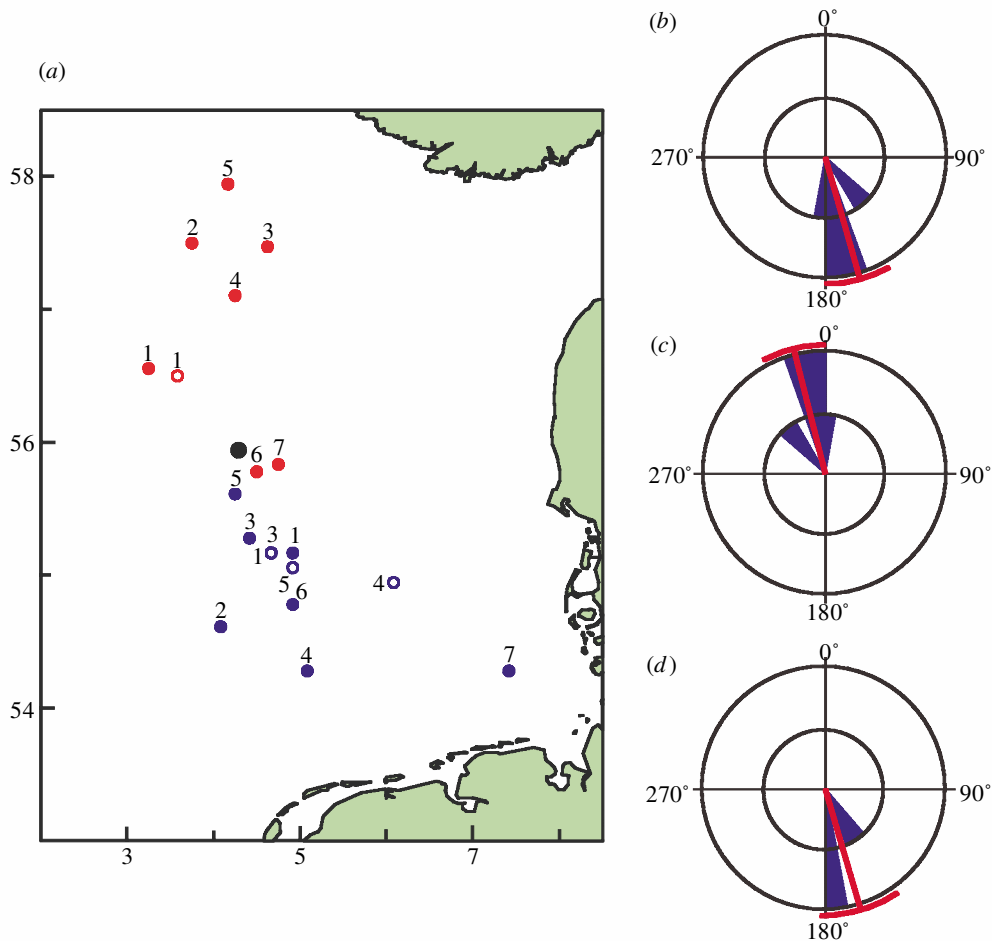
Figure 3. (*a*) Spawning locations and most northerly feeding locations of seven plaice carrying electronic data storage tags, which recorded data over a year or more from December 1997 to April 1999. Rose diagrams illustrate the mean axes (and 95% confidence limits) of migration (*b*) following release to the spawning area (1997–1998); (*c*) from the spawning location to the feeding ground (1998) and (*d*) from the feeding ground to the spawning area (1998–1999). Key: numbers, plaice 1–7; filled red circle, feeding location 1998; open red circle, feeding location 1999; filled blue circle, spawning location 1997–1998; open blue circle, spawning location 1998–1999; filled black circle, midpoint of release.

bank is shown by the rapid movement into shallower water (solid blue line, figure 2*a*(i)). On 25 October, the fish moved up through the thermally stratified layer of water, shown by a marked rise in temperature. The fish then repeated the pattern of the previous year, moving south over the bank (along the peak in depth profile in figure 2*a*), back to the spawning ground and then northward again (broken blue line). Its final geolocation on 28 April 1999 was 11 km from its position a year earlier.

When the behaviours of plaice 1–5 were taken together, they all reached the spawning area within one month of release (27 December 1997 to 22 January 1998). During the southerly pre-spawning migration, they crossed the bank in 34.8 ± 9.9 days in 1997, and 33.7 ± 4.5 days in 1998. In 1998, all five plaice entered a warm water layer on 24–25 October, and temperature increased by *ca.* 2 °C over 4.0 ± 1.6 days. They spent 53.2 ± 24.8 days on the spawning ground. The 1998 post-spawning return trip over the bank took 12.8 ± 2.8 days, and all fish reached their feeding grounds by 13 March 1998.

Figure 2*b*,*c* illustrates two fish that showed variations on the pattern described for fish 1–5 (represented by the individual in figure 2*a*). Geolocations showed that they spent the summer feeding season further south on top of the bank, as verified by the shallower summer depth profile in figure 2*b*(ii) and *c*(ii). Plaice 7 migrated further south and east to spawn than the other fish (figure 2*c*), and recorded rapid, pronounced temperature fluctuation during the summer.

(c) *Migration route and spawning site fidelity*

The northernmost limits of the summer feeding distribution and assumed spawning locations of all seven plaice are shown in figure 3. After release, the plaice followed a mean vector of 164.0° to reach their spawning grounds. This was the same direction as in the second year (163.6°, $n = 4$ fishes that completed the second pre-spawning migration). These fish moved a mean distance of 255.9 ± 60.2 km. The mean direction for the return migration to the feeding areas was 345.8° along a mean distance of 240.8 ± 72.9 km.

The assumed spawning locations of plaice 1 and 3 during the 1998–1999 spawning season were within 15.9 and 20.1 km, respectively, of the previous year's spawning locations, and within 73.5 and 74.7 km for plaice 4 and 5 (figure 3).

4. DISCUSSION

This is the first study to provide a continuous annual reconstruction of migration by individual fish. The plaice in the central North Sea showed strong fidelity to feeding and spawning areas separated by an average of 250 km.

(a) *Migration route and spawning site fidelity*

Philopatry and homing to spawning grounds among broadcast spawners such as plaice is still much less well understood than in diadromous fishes (Groot & Margolis 1991; Metcalfe *et al.* 2002). Rates of homing have been estimated from coarse-scale tagging experiments at between 71% and 95% for herring (McQuinn 1997), cod (Godø 1984; Jónsson 1996) and weakfish (Thorrold *et al.* 2001). Homing in cod is also known to occur on a relatively localized scale (Green & Wroblewski 2000; Robichaud & Rose 2001).

The average predicted level of accuracy of the tidal location method on the spawning grounds was 20–30 km (Hunter *et al.* 2003*a*). The return migration of plaice from feeding grounds 250 km distant from the spawning area, where they were located to within 20 km of their positions during the previous season, suggests a high level of navigational precision by the fish. The precision of our technique might be improved by tagging individuals on spawning grounds with individually coded ultrasonic transmitters, which have already been deployed successfully on homing Atlantic cod (Robichaud & Rose 2001). Our observations of 100% homing rate by four females considerably surpasses the value for cod (26%, allowing for mortality; Robichaud & Rose 2001), although the differences here may be related to scale.

We are not yet able to determine whether the migration route fidelity found here is an example of philopatric homing, with plaice returning to their natal spawning grounds. This distinction could be important for understanding the recently described population substructure of North Sea plaice (Hunter *et al.* 2003*b*). McQuinn (1997) has suggested that the migration behaviour of the Atlantic herring metapopulation is learned via social transmission from mature fish to recruiting individuals. This would both allow plasticity of response to changing environmental conditions and increase the likelihood of colonization events following significant population impacts (in this case fishing pressure).

(b) *Behaviour patterns of migrating plaice*

Increased swimming activity during migration in previous studies of plaice behaviour is associated with the use of selective tidal stream transport (Metcalfe *et al.* 2002). However, the tidal stream currents in the central North Sea are too slow for plaice to be able to take energetic advantage of this behaviour (Hunter *et al.* 2003*b*). Furthermore, the principal vectors of the tidal stream currents in this region run along an east–west axis (Huntley 1980), and therefore do not provide the fish with directional information for the location of their spawning areas. It would therefore appear that mid-water swimming during migration for central North Sea plaice must serve some other, as yet unknown, navigational or social purpose.

The plaice followed the same bearings in the 1998 and 1999 pre-spawning seasons, and the migration of the five

more northerly fish through the thermally stratified layer within 2 days suggests that migration was closely synchronized.

This event further suggests that temperature was not the major cue triggering the onset of migration, as migration was initiated in a thermally stable zone. However, the relative harmonization of movements did suggest an environmental cue. Gibson (1997) suggested that decreasing photoperiod is the likely stimulus. Furthermore, the sharp fluctuations experienced by plaice 7 (figure 2*c*) suggested that thermal stratification probably was not an absolute barrier to plaice movement.

(c) *Relevance to fish stock conservation*

Current fisheries management advice is based on aggregated fisheries data from geographically defined management units, between which no stock mixing is assumed to occur. If the management units cover the full distribution range of the stock, then fidelity to migration routes and spawning areas are implicit in stock assessments. However, it is already recognized that this approach may mask the underlying behaviour of sub-stocks, sometimes leading to localized differential substructure over-fishing (Frank & Brickman 2000). Furthermore, *ca.* 10% of the North Sea plaice stock migrates into an adjacent management area to spawn, then moves back again (L. T. Kell, R. Scott and E. Hunter, unpublished data). Daan (1991) has shown that the assessment of a presumed single stock, which in reality is composed of two or more sub-stocks, will be biased if the sub-stocks are exploited differentially. This effect will be compounded if the mixing is behaviourally underpinned, and may increase the likelihood of localized extinctions (Smedbol & Stephenson 2001; Smedbol & Wroblewski 2002).

Our results demonstrate how the techniques employed here can be used to define the migratory behaviour of free-swimming fishes beyond the simple description of seasonal movements. However, they also underline how little is currently known regarding the fine-scale behaviour and social interaction of seabed dwelling species. We suggest that further studies of this type will assist parameterization of life-history characteristics. These, in turn, can be used to develop more realistic biologically based movement models. Biological models need not necessarily supplant traditional stock assessment models, but may be used as a platform to test them more rigorously (L. T. Kell, R. Scott and E. Hunter, unpublished data). A thorough understanding of the behaviour and spatial dynamics of exploited fish stocks may significantly advance progress towards sustainable exploitation of marine fish stocks.

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