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Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data

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For more than a century, scientists have used mark-recapture techniques to describe the spatial dynamics of marine demersal fish species in the North Sea. Although such experiments have provided extensive data sets, the information is limited to the date and position at release and at recapture. Furthermore, these data may be biased due to the distribution of fishing effort. Recently, electronic (archival) data storage tags (DSTs) have successfully been used to reconstruct the movements of free-ranging demersal fish between release and recapture. Data from DST experiments allow the calculation of fisheries-independent migration parameters, and thereby provide a means of evaluating conventional tagging data. We compared the migration patterns of North Sea plaice (*Pleuronectes platessa* L.) as inferred from a database of twentieth century conventional tagging experiments (CT), with data from 132 plaice tagged with DST. In general, the CT experiments allowed a reliable interpretation of migration patterns, although for certain release areas the migration distances were biased due to the heterogeneous distribution of fishing effort.

Keywords: data storage tags, mark-recapture experiments, North Sea, plaice, *Pleuronectes platessa*.

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Introduction

The spatial dynamics of North Sea plaice (*Pleuronectes platessa* L.) have been examined by fishery scientists for more than a century. A mark-recapture technique had already been described in 1893 (Petersen, 1893), and the first review on plaice tagging experiments was published in 1916 (Borley, 1916). Extensive tagging experiments were carried out in the 1960s and 1970s focusing mainly on spawning populations (De Veen, 1962, 1978; Rauck, 1977; Houghton and Harding, 1978), and in the 1980s targeting juvenile plaice (Lockwood and Lucassen, 1984; ICES, 1992). In total, over 50 000 North Sea plaice were tagged and recaptured during the twentieth century.

Although mark-recapture experiments do not provide information about the extent and direction of movement during the intervening period at liberty, they can provide insight into gross population movements. However, as tagging experiments rely on commercial fishing vessels for tag retrieval, the distribution of recaptures may reflect the commercial fleet's activity more than the true extent of fish migration. This potential bias attributable to heterogeneous distribution of fishing effort can be compensated for by using the number of recaptures per unit effort rather than the total number of recaptures (Rijnsdorp and Pastoors, 1995), or by using more sophisticated methods as proposed by Hilborn (1990). Any method that relates the probability of capture to the distribution of fishing effort depends on the availability of accurate fishing effort data. In the North Sea, the Dutch beam-trawl fleet catches more plaice than any other national fleet, but reliable data on its spatial distribution are available only for the mid-1970s (Rijnsdorp and Pastoors, 1995) and the 1990s (Jennings *et al.*, 1999). Furthermore, no effort data are available to describe the fishing activity of the Belgian and French fleets, both of which play a major role in the flatfish fishery in the English Channel. Despite these limitations, conventional tagging experiments have been used to analyse the population structure and migration patterns of North Sea plaice (De Veen, 1962, 1978; Rauck, 1977; Houghton and Harding, 1978; Lockwood and Lucassen, 1984; Rijnsdorp and Pastoors, 1995). However, in the absence of adequate fishing effort data, it is important to evaluate the accuracy of results derived from the conventional tagging experiments.

Experiments employing plaice tagged with an electronic data storage tag (DST) also depend on the commercial fleet for tag retrieval, but they allow the reconstruction of movements of fish during their free-living period by using the data recorded by the tag (Metcalfe and Arnold, 1997; Hunter *et al*., 2003a). Unlike recapture positions, these positional estimates, or geolocations, are independent of the spatial distribution of the fishing fleet. The experiments conducted using DSTs therefore allowed an effectively fisheries-independent means of calculating migration parameters against which the migration parameters derived from conventional tagging (CT) data could be compared.

Methods

Tagging experiments with electronic data storage tags (DSTs) were conducted in several areas of the North Sea covering the major distribution area of plaice. The DSTs employed were programmed to record depth (pressure) and temperature every 10 min. When the fish remains motionless on the seabed, the depth measurements register a sine-wave related to the rise and fall of the tide. The tidal ranges (high to low water) and the time of high water were extracted from the recordings with a wave-fitting algorithm. An oceanographic model was used to produce a tidal database for the entire North Sea and eastern English Channel on a 12 by 12 km grid. This database was used to identify locations with tidal ranges and times of high water comparable to those recorded by DST on a given date. The tidal data were matched within tolerance limits that reflect the known depth resolution (± 20 cm) and sampling rate (10 min) of the DSTs, and the assumed uncertainty of the tidal data predicted by the oceanographic model (± 15 cm and ± 20 min). Sometimes the recorded tidal data were not conclusive because they corresponded with geographically distinct positions. Incorrect positions could be eliminated by comparing seabed depths or – in the case of non-stratified waters – sea surface temperatures at the derived locations with the actual depths and temperatures recorded by the tags. This method in which the geographic location is derived from environmental variables is described in detail by Hunter *et al.* (2003a). They examined the accuracy of the method and concluded that the geolocations over much of the North Sea and English Channel were accurate within 40 km. A total of 1015 geolocations was available from 132 DST plaice. Individual fish provided multiple observations and in some cases several geolocations per month. As geolocations can only be obtained when the fish remains motionless on the seabed, the distribution of all geolocations will probably over-represent the non-migratory period of the life cycle. To avoid bias in the geographic distribution caused by this uneven sampling throughout the year, only one geolocation per month at liberty (the midpoint) was included for each individual. This gave a final sample size of 580 geolocations that can be treated as "virtual recaptures".

The DST data were divided into eight experiments, each corresponding to one or more of the original DST experiments. The area and period of release, and the number of individuals (recaptures) and geolocation positions are listed in Table 1. Figure 1 shows the locations of the areas that are referred to in this paper. Only plaice with a minimum total length of 35 cm were tagged with DSTs. Each DST experiment was complimented with a conventional tagging (CT) "experiment". This was an extraction from the conventional tagging database, corresponding (where possible) to the DST experiment release conditions. Experiments were defined with the same release area (at ICES rectangle level), and in all but two cases (experiments B2 and B3), the same release months. Only plaice larger than 35 cm were included in the CT experiments. Sex differences were ignored (only one of the DST plaice was male, compared with 27% of the CT fish). The year of release was also not considered as a selection criterion. The geographic distributions of the recaptures of the CT experiments were compared with the geolocations of the DST experiments.

The distance travelled by a group of fish between spawning areas and feeding grounds was quantified using the parameters mean distance and group displacement. Group displacement is the distance between the release position and the centre of density of a group of tagged fish, and was calculated according to the formulae presented by Jones (1959, 1976). The spawning season was defined as January to February (Harding *et al*., 1978). Geolocations within the spawning season had been obtained for only 54 DST plaice. For these individuals, the southernmost geolocation during the spawning period was defined as the spawning location. Most of these points (43) were on spawning grounds in the south-eastern North Sea, and they were treated as virtual "spawning releases". The migration parameters of these DST spawning releases were then compared with those of CT spawning releases. Selection criteria for the CT data set were release size (>35 cm), release period (January–February), and release area (south-eastern North Sea), resulting in a total of 1719 recaptures. The group displacement and the mean distance by month, for a period of 12 months after spawning, were calculated separately for the three spawning regions in the

Table 1. For each pair of conventional tag experiment (CT) and data storage tag experiment (DST), the release conditions (ICES rectangles, months, years), the number of individuals recaptured, and the number of positions recorded (CT: recapture position; DST: only one geolocation position per month at liberty).

Experiment		Tag	Releases in			Number of	
			ICES rectangles	Months	Years	Recaptures	Positions
A1	Southern Bight	DST	33F2, 34F2	Dec–Jan	1993, 1996–1997	22	64
		CT	34F2	Dec–Jan	1959–1960, 1991–1995	67	67
A2	Southern Bight	DST	34F2	Feb	1998	9	56
		CT	34F2	Feb	1998	101	101
A3	Southern Bight	DST	33F3	Feb	1999	7	33
		CT	33F3, 34F3	Feb	1960–1961, 1972, 1975	107	107
B1	Central North Sea	DST	41F5	Oct	1997	16	66
		CT	41F5–F6	Oct	1997	29	29
B2	Central North Sea	DST	40F4, 41F4	Dec	1997	40	193
		CT	40F4	May	1946–1954, 1958	268	268
B3	Central North Sea	DST	42F3, 43F2–F3	Oct	1998	7	27
		CT	43F3	Apr, Jul	1911, 1957	35	35
C	German Bight	DST	38F6, 39F6–F7	Oct–Nov	1997	20	95
		CT	38F6, 39F6–F7	Oct–Nov	1947, 1973, 1997–1998	52	52
D	Flamborough	DST	37F2, 38F1	Sep–Oct	1998–1999	11	46
		CT	37F1, 38F1	Aug–Sep	1907, 1947, 1963	83	83

south-eastern North Sea: Southern Bight, German Bight, and Dogger Bank region.

Results

Figure 2 shows the geographic distribution of geolocations (DST) and recapture positions (CT) of the eight paired experiments listed in Table 1. Note that each recapture symbol in the CT maps corresponds to a single individual, whereas several geolocations (DST) may originate from the same fish.

For all of the Southern Bight releases, the overall distribution produced by the DST and CT experiments was similar (Figure 2a). Most plaice released in the western Southern Bight (experiments A1 and A2) moved along a north to northwest axis, whereas the eastern Southern Bight releases (experiment A3) generally moved north to northeast. Only 7 (4%) of the 168 CT plaice released in the western Southern Bight (experiments A1 and A2) were recaptured in the eastern part of the North Sea: five were recaptured in the Fisher Bank region (experiment A2) and two were recaptured off the Frisian Islands (experiment A1). None of the 31 DST fish from releases A1 and A2 entered the eastern part of the North Sea. Note that the CT and DST fish in experiment A2 originated from the same release (Table 1).

Eight of the DST plaice tagged in December–January (experiment A1) moved south into the eastern English Channel (36%). This was a larger proportion than was observed with the CT fish (13%). Two individuals from release A2 (February) entered the eastern English Channel. These were the only two DSTs from this release to record all the way through to the following spawning season. Although these represent just 22% of fish in this experiment, they account for 100% of the fish that recorded data during the subsequent spawning season.

In a number of experiments in which relatively few DSTs were returned, but which had recorded long time-series of data, clusters of geolocations from individual fish were clearly identified. This was particularly evident in experiment A3 in which two of the seven DST plaice recorded data over protracted time periods and followed clearly distinct migration pathways. One of these individuals migrated north after release in February and remained in the central North Sea until December, it then moved back to the Southern Bight and was caught in the vicinity of the release position next February. The other individual migrated to the northwestern side of the Dogger Bank and was captured there almost six months after release (Figure 2a). A distinct individual track was also observed in experiment A2, in which a single plaice moved into Scottish waters where it remained on Aberdeen Bank for six months until capture (Figure 2a and Figure 3 in Hunter *et al.*, 2004a).

The distribution of recaptures and geolocations from the central North Sea releases (experiments B1–B3) show

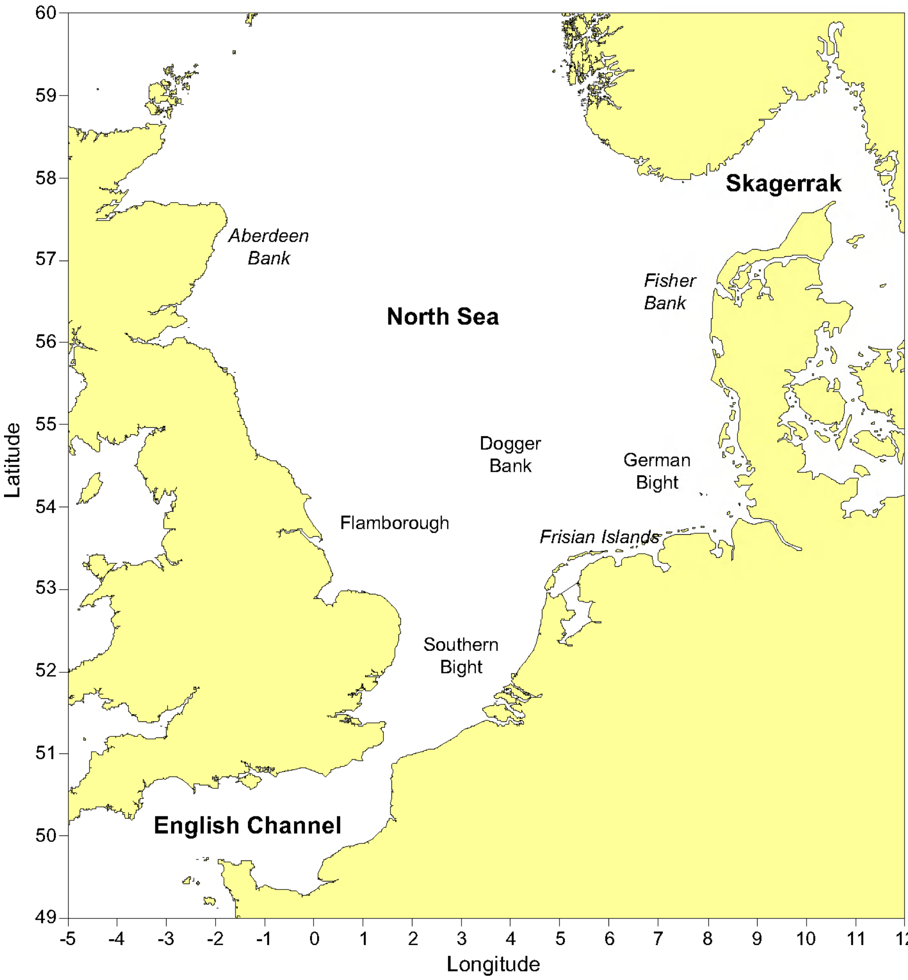


Figure 1. Map of the North Sea showing the areas that are referred to in the description of the tagging experiments and migratory movements of plaice.

similar patterns (Figure 2b). However, slight differences were observed for experiments B2 and B3, where the range of CT recaptures appeared to be further north than the range of geolocations (DST).

The distributions of both CT and DST fish in the German Bight (experiment C) demonstrated that both groups of fish migrated into the Southern Bight, although the results from the CT fish suggested a greater degree of spread to the north and to the west (Figure 2c). The overall distribution pattern was also similar for plaice released off Flamborough (experiment D), although the overall range was again more extensive in CT experiments than in DST experiments (Figure 2c).

The group displacement and the mean distance travelled in the 12 months following spawning were estimated separately for the Southern Bight, Dogger Bank, and German Bight spawning regions. In the DST experiments each individual fish could provide more than one observation in total, but never more than one observation per month. The migration patterns in terms of group displacement (not plotted) were similar to the mean distance travelled (Figure 3). Comparison between the DST and CT results showed that both group displacement and mean distance travelled were significantly different in the Southern Bight. No significant differences were observed in the German Bight or Dogger Bank regions (Table 2 and Figure 3). Data from the DST experiments suggested that plaice spawning in the Southern Bight were migrating over substantially greater distances than fish spawning in other regions of the North Sea. The estimated group displacement six months after spawning varied between 80 and 120 nautical miles for plaice spawning in the German Bight and Dogger Bank area, and according to the CT experiments, also for plaice spawning in the Southern Bight. The DST experiments, however, estimate a group displacement of approximately 220 miles for plaice spawning in the Southern Bight.

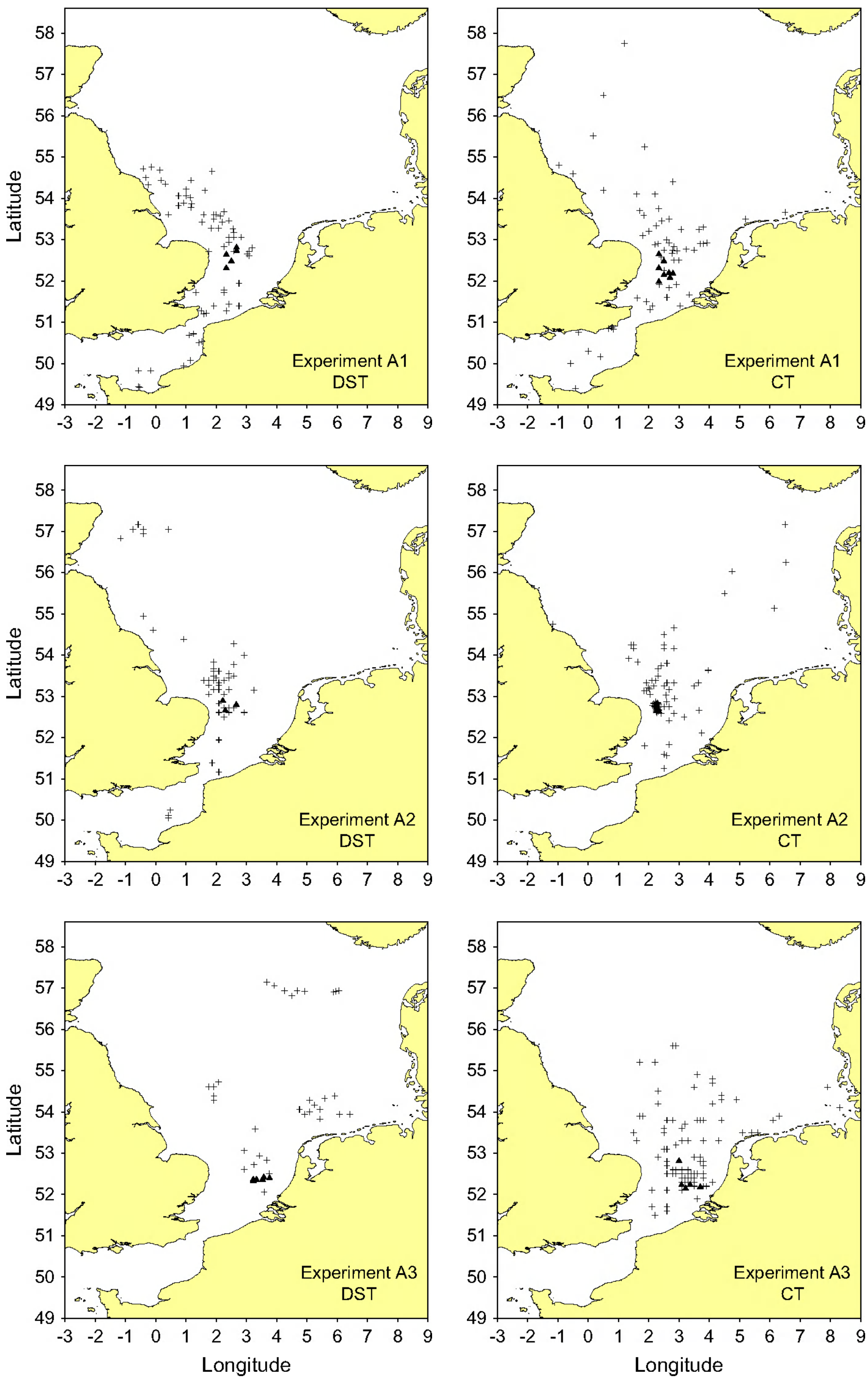


Figure 2. Geographic distribution of recaptures in conventional tagging experiments (CT) and geolocations in data storage tag experiments (DST), for plaice released in different parts of the North Sea (▲ = release position; + = recapture position/geolocation). (a) Southern Bight releases; (b) Central North Sea releases; (c) German Bight and Flamborough releases.

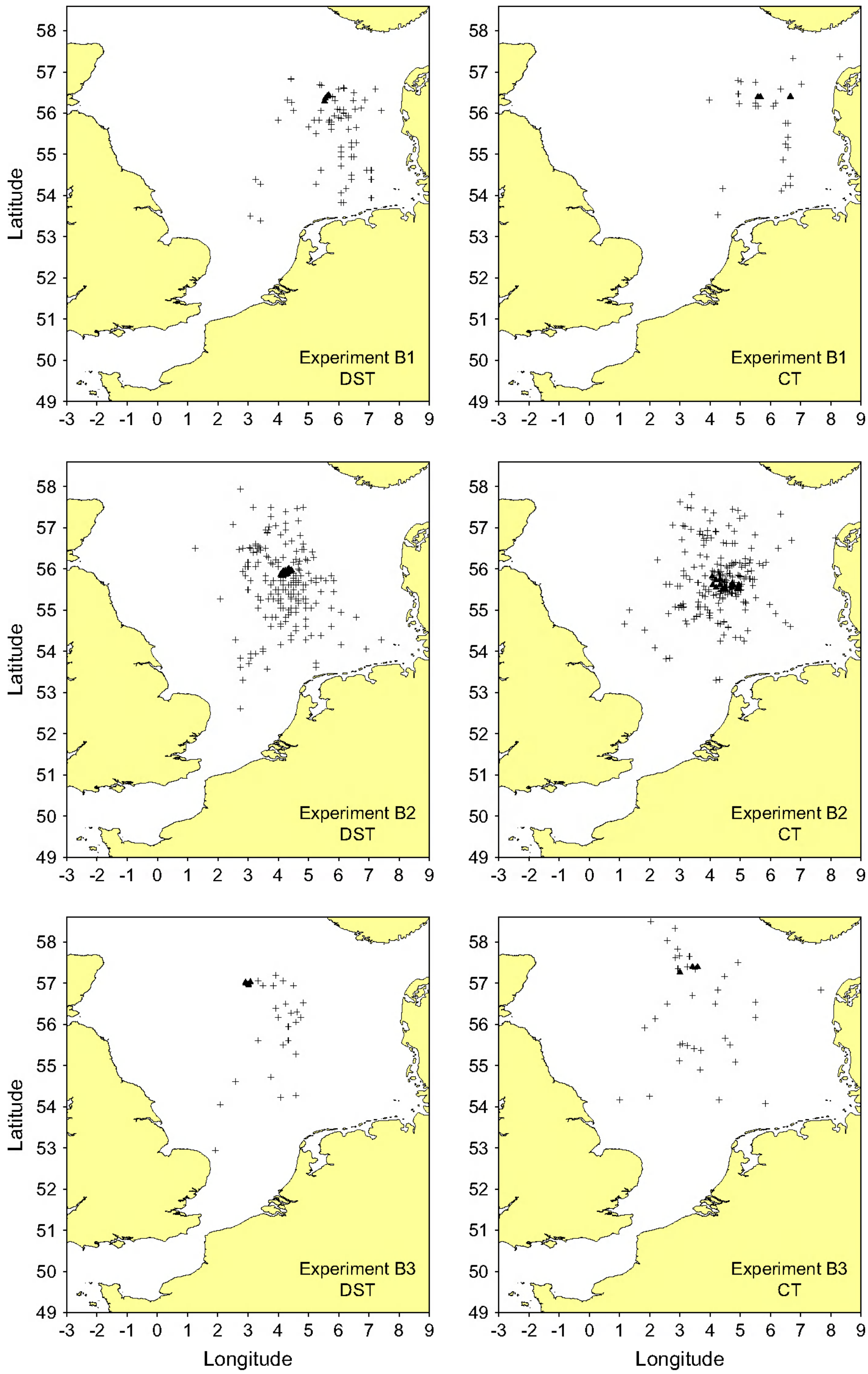


Figure 2 (*continued*)

Discussion

The results of DST experiments were used to evaluate population migration patterns derived from CT experiments. In principle all other variables that may influence the extent and direction of migration should be the same when comparing DST and CT results, but in practice this proved to be impossible. Most important factors to take into

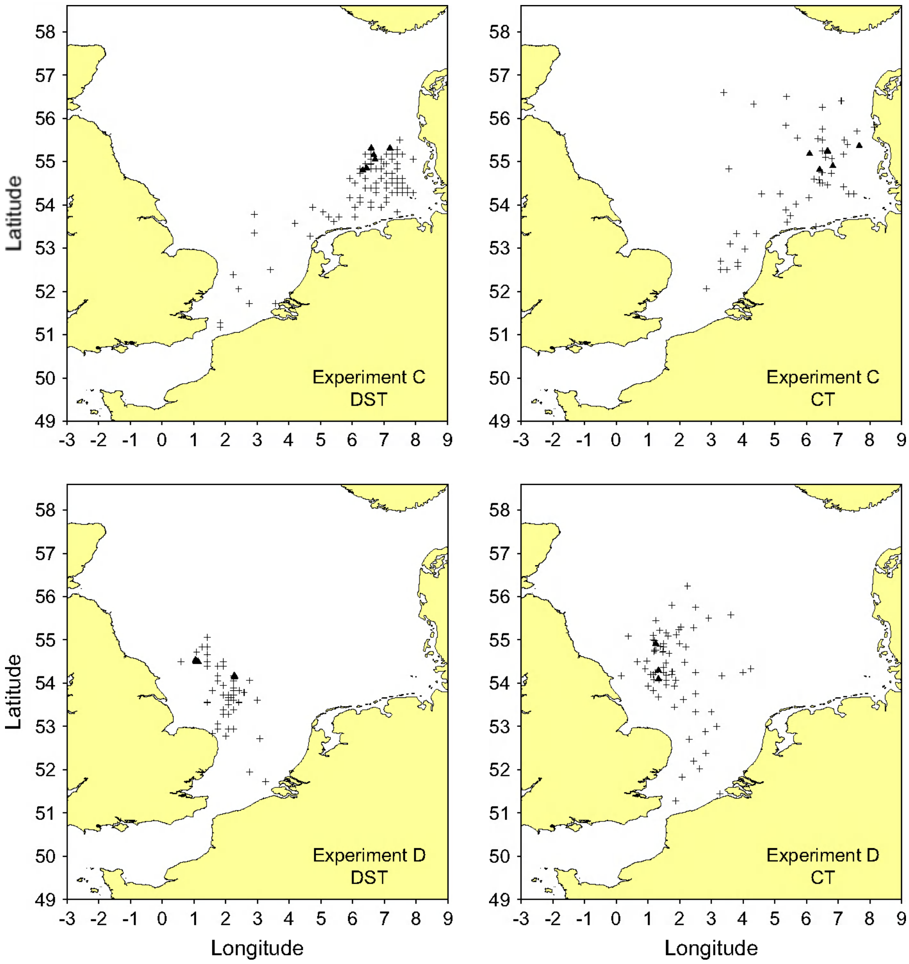


Figure 2 (*continued*)

consideration, given the strong seasonal migration patterns in plaice, are the time and location of release. Furthermore the size of the fish affects the extent of migration with larger fish travelling substantially greater distances than smaller fish (LB, pers. obs.). These factors were taken into account in the selection procedure of CT data, but sex and year of release were not. Almost all DST fish were females whereas 27% of the CT fish were males. On average, males appear to migrate greater distances than females, but this is probably related to the earlier maturation of males. Consequently, in plaice larger than 35 cm, the difference between males and females is small. Ideally, year of release should have been included in the selection criteria, but insufficient CT data were available. Although no indications of substantial changes in adult migration patterns exist (De Veen, 1962; Rijnsdorp and Pastoors, 1995; LB, pers. obs.), the distribution and level of fishing effort have changed over time (Jennings *et al.*, 1999; ICES, 2004).

The DST results illustrate the limitations of using (small) DST experiments to describe population migration patterns, given the ability on occasion to identify individual tracks within the plots of geolocations. Individuals occasionally deviate strongly from the general migration pattern. If such individuals record data over a long time period, then the distribution range can be skewed, especially if the experiment consists of few individuals. For example in experiment A3 (Figure 2a), the six southernmost DST plaice effectively described the extent of the observed recapture distribution of CT fish. Only one DST plaice migrated further north to the central part of the North Sea, where no CT fish were recaptured.

In general we found that the range over which DST fish were located and the areas from which conventionally tagged fish were returned were largely similar, especially within the range of 75% of the recaptures/geolocations. Despite the overall similarity, some differences between the data sets were observed which required further attention.

Table 2. ANOVA table of the effect of time after spawning (months) and tag-type (DST or CT) on the estimation of group displacement and mean distance travelled. Model: $Y = \alpha \times \sin(t) + \beta \times tag + \chi$, in which Y = mean distance or group displacement; $t = (months/12) \times \pi$; tag = class variable DST or CT.

		Group displacement			Mean distance		
Source	d.f.	SS	F	p	SS	F	p
Southern Bight							
Error	18	20 887			16 231		
sin(t)	1	41 652	35.9	<0.001	35 073	38.9	<0.001
Tag	1	31 769	27.4	<0.001	26 060	28.9	<0.001
Dogger Bank							
Error	20	6 520			4 084		
sin(t)	1	13 954	42.8	<0.001	10 375	50.8	<0.001
Tag	1	173	0.53	0.474	324	1.59	0.222
German Bight							
Error	20	8 850			4 816		
sin(t)	1	11 275	25.5	<0.001	9 135	37.9	<0.001
Tag	1	453	1.02	0.324	2	0.01	0.931

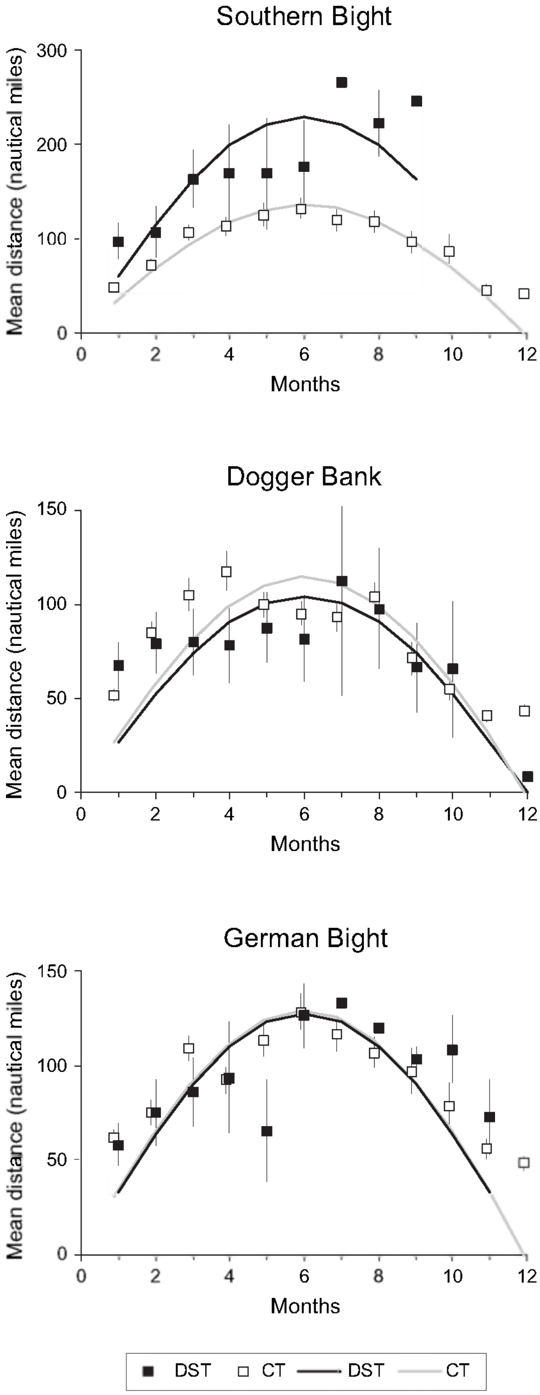
DST results showed that approximately one-third of the plaice released in the Southern Bight visited the eastern English Channel. The observed differences between the DST and CT results may at least partially be explained by the behaviour of these fish during spawning. Plaice in the Southern Bight use selective tidal stream transport to migrate, while plaice in the German Bight and central North Sea do not use this transport mechanism (Hunter *et al.*, 2003b, 2004a, 2004b). This behaviour may have two implications for the present results. Firstly, tidally transporting plaice spend significantly more time off the seabed during migration, and may therefore be less available to capture by bottom trawl during the migratory period. Secondly, DSTs demonstrate that the majority of plaice reaching the eastern English Channel spawning grounds rarely remain there for longer than six weeks before returning to the North Sea. Although we have insufficient data at present to determine the levels of fishing effort in the eastern English Channel, it seems plausible that the low levels of recapture from this area may result from lower levels of fishing effort, possibly in combination with reduced catchability.

An unexpected result from release A2 (Figure 2a) was the recapture of five CT plaice from the eastern North Sea. These fish originated from the same tagging cruise as the DST fish, none of which ever left the western North Sea. Inaccuracy of the recapture positions is possible, because the tags are retrieved by commercial vessels. However, the five tags were recaptured by different vessels and it seems unlikely that all these vessels made errors in the registration of the recapture position. The difference is probably due to chance alone, as experiment A2 contained 101 CT plaice, but only nine DST plaice.

The DST and CT data sets for central North Sea fish were largely consistent, although the CT plaice from two of these releases (experiments B2 and B3) appeared to be distributed slightly further to the north. These differences were most probably related to differences in the release months (Table 1). The DST plaice were released at the end of the feeding season (October—December) shortly before their southward migration towards the spawning grounds, whereas the CT plaice were released at the beginning or middle of the feeding season (April—July).

DST experiments have revealed that the population structure of North Sea plaice may be related to the distribution of thermal stratification during summer (Hunter *et al.*, 2003b, 2004a). The DST fish in experiment C appeared to have been released at the northernmost limit of their distribution. The release position was in the immediate vicinity of a transitional thermal area (the southernmost limit of the thermally stratified layer). All DST fish from release C remained in the thermally mixed zone to the south of the thermal front (Figure 2c). The CT data points from experiment C (Figure 2c) may have partly been derived from a more westerly release in deeper, cold stratified water. These fish would therefore belong to the same subgroup sampled by releases B1—B3 (Figure 2b). The influence of physical factors on population distribution at this scale cannot be discriminated using CT data.

Group displacement and mean distance were calculated in order to quantify any differences in overall migration patterns identified from the visual inspection of the recapture and geolocation maps. The DST data indicate that plaice spawning in the Southern Bight migrate over greater distances than was estimated from the CT data. Such differences were not observed for plaice spawning in the German Bight or in the Dogger Bank regions. The quantitative comparisons between DST and CT should be treated with caution, however, as DST experiments were



Southern Bight

month	DST	CT
1	9	89
2	8	71
3	5	61
4	5	47
5	3	44
6	3	40
7	1	34
8	2	34
9	1	22
10		18
11		54
12		59
recaptures	12	573

Dogger Bank

month	DST	CT
1	20	108
2	17	45
3	11	39
4	11	29
5	9	49
6	8	50
7	2	42
8	3	28
9	3	23
10	2	45
11		111
12	1	72
recaptures	20	641

German Bight

month	DST	CT
1	9	86
2	7	62
3	6	39
4	4	48
5	3	34
6	2	21
7	1	29
8	1	31
9	2	17
10	2	25
11	2	47
12		66
recaptures	11	505

Figure 3. Comparison of the distance travelled in the 12 months after spawning according to data storage tag experiments (DST) and conventional tagging experiments (CT), for plaice spawning in the Southern Bight, Dogger Bank region, and German Bight. The symbols present the mean distance travelled (±s.e.) for each month, and the curves present the fitted values according to the model described in Table 2. The total number of individuals recaptured and the number of observations for each month are listed (CT: months at liberty; DST: months after spawning).

based on relatively few observations and even fewer individuals (Figure 3). One of the 12 DST fish in the Southern Bight spawning group was released in the German Bight (experiment C). It spawned in the Southern Bight, and within three months migrated ~250 miles to ~55°N–7.4°E, where it remained until recapture. This individual provided 9 of 37 observations (24%). If this individual had been omitted from the data set, the differences between the DST and CT experiments would be much smaller, although still statistically significant.

The Southern Bight data set contained all DST fish that spawned in the Southern Bight irrespective of release position. Plaice that were released in the Southern Bight and spawned in the eastern English Channel were not included. Therefore, our previous observation that more plaice entered the eastern English Channel according to the DST data, did not account for the differences in group displacement. The CT experiments appear to have underestimated the overall distance travelled by plaice spawning in the Southern Bight. This bias is most probably caused by the spatial distribution of fishing effort. Bottom-trawling effort is highest in the south-eastern North Sea and rather low in the central North Sea (Jennings *et al.*, 1999). Hence, individuals moving into the central North Sea will have a much lower probability of being captured.

In general, DST tagging experiments largely confirm the migration patterns and population structure of adult plaice as inferred from the conventional tagging experiments (De Veen, 1962, 1978; Rijnsdorp and Pastoors, 1995; Hunter *et al.*, 2004a; LB, pers. obs.). Evaluation of juvenile CT experiments using DST data is not yet possible, because at present only large fish (>35 cm) have been tagged with data storage tags. Although the general patterns were similar, the comparison of CT and DST experiments showed subtle differences between the two data sets. The most evident difference was the suggestion that the extent of migration from the Southern Bight may have been underestimated by conventional tagging experiments. DST data provide more information on individual migration patterns and the physical data recorded by the tag have further allowed the interpretation of spatial distributions, which would not otherwise have been apparent from CT data. Nevertheless, it has been shown that large mark-recapture data sets can provide important information with regards to general migration patterns and population structure. It is concluded therefore that conventional tagging experiments "tell the truth, but not the whole truth".

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