Impacts of migratory behaviour on population structure in North Sea plaice

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Summary

1. Migration is widespread among marine fishes, yet little is known about variation in the migration of individuals within localities, and the consequences for spatial population structure. We tested the hypothesis that variation in the migratory behaviour among plaice (*Pleuronectes platessa* L.) in the North Sea could be explained by large-scale differences in the speed and directions of the tidal streams, which the fish use as a transport mechanism.

2. We released 752 mature female plaice tagged with electronic data storage tags at eight locations with contrasting tidal flow properties between December 1993 and September 1999.

3. The experiment yielded 20 403 days of data from 145 plaice. Individual tags recorded depth and temperature for up to 512 days. The position of each fish was determined at intervals throughout the liberty period using the tidal location method.

4. The results show that the fish were segregated into three discrete feeding aggregations during the summer non-breeding season. Two clusters were in warm, thermally mixed water in the eastern and western North Sea, respectively, and one was in deeper, cold, thermally stratified water to the north.

5. In the winter spawning period, fish from all three aggregations mixed together in the southern North Sea, and fish from the eastern and northern subunits spawned in the south-eastern North Sea. The only fish that left the North Sea were western subunit plaice that visited spawning grounds in the eastern English Channel.

6. Our results re-affirmed the major role of the tidal streams in the southern North Sea in structuring plaice dispersion, both by providing transport and guidance and by delimiting the extent of distribution due to thermal stratification during the summer. However, plaice from the northern North Sea did not use tidal stream transport.

7. These results confirm the prediction that large-scale variation in migration behaviour can be explained in part by the tidal guidance and transport mechanisms available. They have also revealed features of spatial dynamics not observed previously from a century of conventional tagging experiments and illustrate how the study of individual fish can successfully define the migratory characteristics of populations.

Key-words: bird migration, data storage tags, fisheries, fish behaviour, flatfish, spatial dynamics, thermal stratification.

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Introduction

Long-distance migration is a prominent feature of the behaviour of many taxa, including fishes, birds, mammals and insects. Among the many definitions of 'migration', it is generally accepted that migration involves the movement of individuals and populations from one well-defined area of habitat to another, usually on a cyclical basis (e.g. annual, Alerstam 1990; Metcalfe, Arnold & McDowall 2002). Migration is expected to evolve when the quality of sites varies in suitability for different parts of the life cycle, such as breeding and foraging. Therefore it is well known that

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most temperate breeding bird species make predictable long-distance migrations between their breeding grounds and foraging sites. Indeed, most of our understanding of the costs and benefits of long-distance migration come from avian studies (e.g. Alerstam 1990; Berthold 2001; Wernham *et al.* 2002). A typical feature of avian migration is that birds from discrete or adjacent breeding grounds often converge onto overlapping wintering areas (Alerstam 1990; Berthold 2001). For example, many species that breed across wide latitudes in northern North America undergo a funnel-shaped migration as they converge into small regions of Central America for the winter (Berthold 2001).

It is less well known that hundreds of marine fish species also undergo long-distance migration (Metcalfe *et al.* 2002). Indeed, the top 15 most economically important species including Peruvian anchovy (*Engraulis ringens* Jenyns), chub mackerel (*Scomber japonicus* Houttuyn) and Atlantic cod (*Gadus morhua* L.) all undergo extensive migrations (Harden Jones 1968; Novikov 1986; Ben-Tuvia 1995). White sharks (*Carcharodon carcharias* L.) and Atlantic bluefin tuna (*Thunnus thynnus* L.) can make trans-oceanic migrations of thousands of kilometres as part of their annual cycles (Block *et al.* 2001; Boustany *et al.* 2002).

We know far less about migratory patterns and processes in oceanic fishes than we do in birds, due to the well-known problems of marking and recovering large numbers of individuals (Metcalfe *et al.* 2002). Furthermore, the consensus for traditional mark–recapture experiments with bottom-dwelling species is that recaptures describe the distribution of fishing fleets more accurately than the true extent of fish dispersion (Hilborn 1990; Rijnsdorp & Pastoors 1995; Bolle *et al.* 2001). Studies of fishes have therefore lagged well behind those of birds in understanding individual variation in migratory behaviour, and consequences for population subdivision and convergence on the breeding and non-breeding grounds.

In this study, we take advantage of new technologies that have enabled us to reconstruct the movements of plaice (*Pleuronectes platessa* L.) between summer feeding grounds in the northern North Sea and winter spawning areas in the southern North Sea and English Channel. We used computerized data storage tags, which allow detailed reconstructions of movements of individuals (Metcalfe & Arnold 1997; Hunter *et al.* 2003a, 2004). We know that fish in some locations use tidal streams as transport and guidance mechanisms during migration (Greer Walker, Harden Jones & Arnold 1978; Hunter *et al.* 2004). We also know that in the north-central North Sea, the tidal currents are probably too weak to be useful for either guidance or for saving energy (Metcalfe, Arnold & Webb 1990). Here we ask two related questions: first, how do the fish behave in areas where tidal streams are unsuitable as aids for migration, and secondly, what are the consequences of the interplay between spatial variation in such physical processes and behavioural decisions of fish for population subdivision or aggregation in wintering and summer grounds.

Methods

TAGS AND TAGGING

We deployed 452 Lotek LTD-1200 (Lotek, Ontario, Canada) electronic data storage tags on plaice at eight North Sea locations between October 1997 and September 1999 (Fig. 1). The tags weighed 16 g in air (2 g in sea-water), and were attached to mature, predominantly female (99%) plaice with a minimum total length of 35 cm. The tags were programmed to record depth (pressure) and temperature every 10 min. Battery power provided a maximum possible recording time of approximately 18 months.

Tagged fish were caught by beam trawl from dedicated research vessels and commercial trawling boats. Only fish in the best condition after capture were tagged. Where possible, tagging tows did not exceed 30 min, and a large trawl mesh (90 mm) was used throughout. All tagged fish were released shortly after capture, usually with a turnover time of 30 min. Roughness of the skin (through lack of slime), missing scales, bruising and bloodying of the tail all provided evidence of physical damage. General sluggishness was also taken as evidence of low survival probability. These features were generally apparent 15 min after capture, and allowed rapid elimination of individuals unsuitable for tagging.

In light of previous work demonstrating the relationship between the migrations of plaice in the southern North Sea and the highly polarized, fast-flowing tidal currents that occur there (reviewed by Arnold & Dewar 2001), we aimed to release fish over as wide a geographical area as possible, but also incorporating areas with contrasting tidal flow properties. Specifically, release locations (Fig. 1), were chosen based on the following criteria: (a) lack of existing data (locations 1, 2, 3, 5, 6, 8); (b) very slow average tidal current velocity (locations 1, 3 and 6); (c) intermediate average tidal current velocity (locations 2 and 5); (d) fast average tidal current velocity, English coast (locations 4 and 8); and (e) fast average tidal current velocity, Dutch coast (location 7).

We have also incorporated data from fish released by the CEFAS laboratory with 302 data storage tags of an earlier design. The tags weighed 55 g in air (23 g in sea water) and were attached to female plaice at least 40 cm long. Depth was recorded at 10-min intervals and temperature was recorded daily, allowing for a potential recording duration of 222 days. Following initial capture, plaice in these studies were returned to the laboratory aquarium in Lowestoft, UK to acclimate, where they remained for 43 ± 20 days before tagging and release at sea. These fish were released between December 1993 and February 1997 (Metcalfe & Arnold 1997; Metcalfe *et al.* 1999) in the vicinity of release location 4 (Fig. 1).
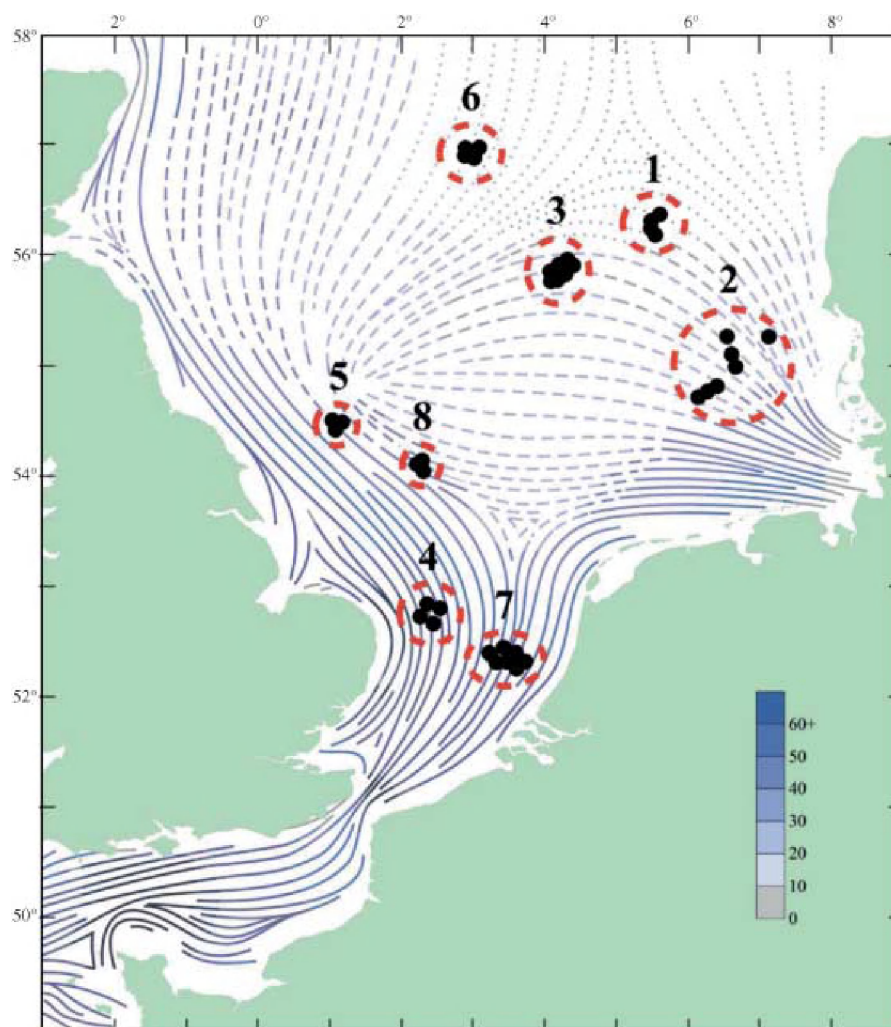
Fig. 1. Release locations of mature female plaice (*Pleuronectes platessa* L.) tagged with electronic data storage tags. Each dot represents a release point. Lines indicate the direction of tidal flow. Colours indicate average tidal current velocities across the study area (scale units = cm^{-1}). Release 1, 29/10/97–30/10/97; release 2, 29/10/97–13/11/97; release 3, 5/12/97–6/12/97; release 4, 17/02/98–20/02/98; release 5, 9/10/98; release 6, 9/10/98; release 7, 15/02/99–25/02/99; release 8, 22/09/99–23/09/99.

Raw data were downloaded when the tags were returned, and converted into depth (m) and temperature (°C). The depth record was filtered to remove periods of mid-water activity, indicated by instantaneous depth changes of 3 m or more, allowing determination of sea-bed depth (Hunter *et al.* 2003a). For each tag, we calculated mean daily sea-bed depth and temperature (± SD).

DESCRIBING SPATIAL DISTRIBUTION USING THE TIDAL LOCATION METHOD

When tagged fish spent one or more tidal cycles resting on the seabed, it was possible to estimate geographical location using the tidal location method (Metcalfe & Arnold 1997; Hunter *et al.* 2003a). Times of high water and tidal range were measured from the depth record, and were compared with a tidal database derived from a 12-km resolution numerical model (see Hunter *et al.* 2003a for details). The database was used to identify all positions with matching times of high water and tidal

ranges measured by the tag on any given date. We could not detect times of high water and tidal range when the fish became active or swam into mid-water (Hunter *et al.* 2003a).

The accuracy of the method is related to the rate of change of tidal parameters at any given point in the North Sea (Hunter *et al.* 2003a). The level of predicted accuracy was reflected by the degree of spread of the estimated positions, ranging from single points to small clusters of positions (not usually greater than 40 km across). For the purposes of this study, when the method generated clusters we calculated the geometric mid-point of the cluster, which was taken as the assumed location of the fish. The method sometimes also generated geographically distant locations for the same tidal data (see Hunter *et al.* 2003a); incorrect locations were eliminated by comparing the estimated positions with sea-bed depths (taken from British Admiralty Charts) and averaged sea-surface temperatures (prepared weekly by Bundesamt für Seeschiffahrt und Hydrographie, e.g. see Loewe 1998).

During active migration, periods of 2 weeks or more sometimes elapsed before fish spent an extended period on the sea-bed. By contrast, outside the migration season, many fish rarely left the sea-bed, producing continuous records of tidal parameters over a period of months. Where possible we aimed to use the tidal location method with a minimum interval of 2 weeks from October to May, and at monthly intervals during the summer months. Within this framework, we further attempted to estimate position following all protracted movements.

We assumed that during the spawning and migration season (November–April), all fish that exhibited polarized movement to and from a distant position within their overall range had performed a pre- and post-spawning migration. In such cases the limit of distribution (the most distant location) was assumed to be the spawning location of the fish.

ANALYSIS OF SPATIAL DISTRIBUTION

We performed a cluster analysis to compare the feeding and spawning distributions of plaice and to examine the role of physical factors in structuring the distributions observed. We compared data from geolocations made in June, when plaice are on their summer feeding grounds, with data from January, when peak spawning occurs. Using the *mclust* and *mclass* functions in S-Plus, cluster analysis was performed using depth and temperature as functions. Only the first observation per fish per month was used, and depths and temperatures were standardized with means of zero and standard deviations of 1. The number of clusters identified was based on approximate weight of evidence plots. The point at which the approximate weight of evidence reaches its maximum indicates the probable number of clusters.

In order to test the null hypothesis that no classification existed between the group classification in January and the group classification in June, a Fisher's exact test was performed on the data from those fish that were common to both data sets.

Results

The data presented comprise 17 447 days of fish behaviour (111 plaice) from the current study and an additional 2956 days (34 plaice) returned from electronic tags released by CEFAS between 1993 and 1997.

SEASONAL DISTRIBUTION OF TAGGED PLAICE

Composite monthly plots of all estimated positions for 144 of the 145 fish are shown in Fig. 2. Fish exhibited minimal lateral movement during the summer feeding season (June–October), therefore these positions were plotted together. Our results indicate a three-way geographical division of the sampled North Sea population during the feeding season (Fig. 2, 1st panel). Geographically distinct subgroups were located in the western ($n = 52$ plaice), eastern ($n = 21$ plaice) and northern North Sea ($n = 64$ plaice). Only a single individual from release position 4 (Fig. 1) migrated north into Scottish waters, where it spent the summer on Aberdeen Bank (57°N, 0·5°E, Fig. 3). No fish were found north of 58°N (Fig. 2).
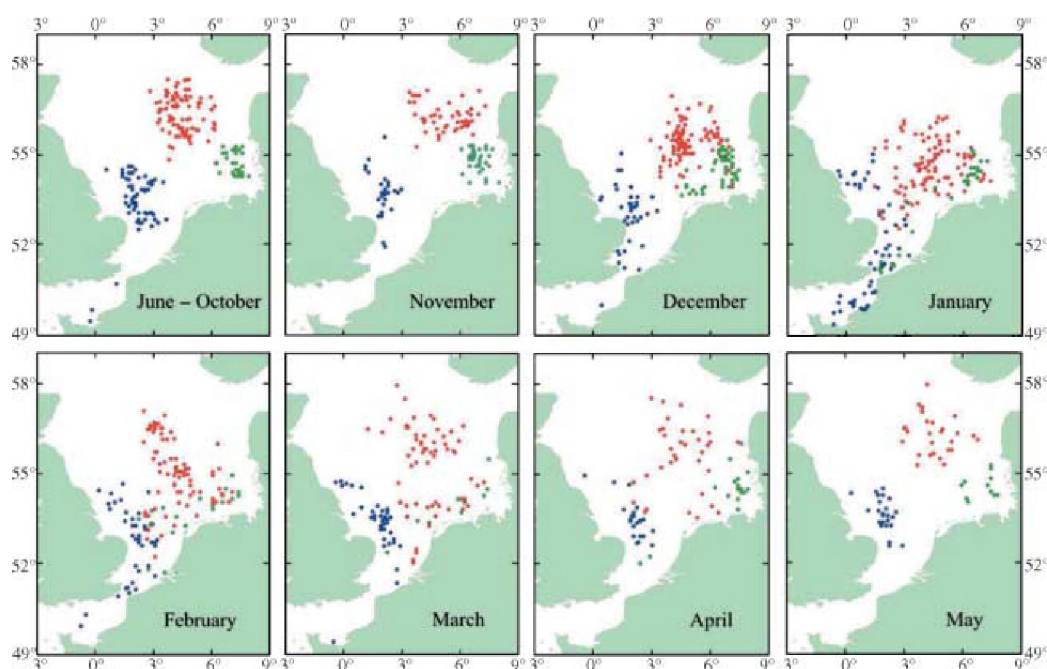
Fig. 2. Monthly composite plots of locations for 144 plaice carrying electronic data storage tags. Each filled circle represents a single location calculated from tidal data recorded when fish remained on the seabed for a full tidal cycle (see text for details). Western subunit = blue; eastern subunit = green; northern subunit = red.
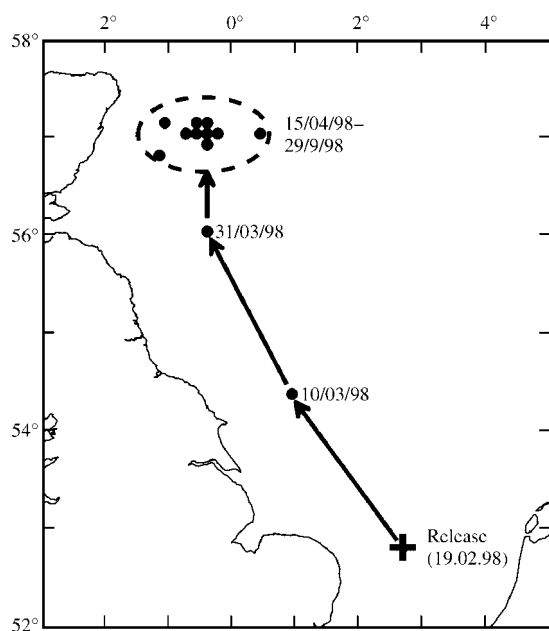
Fig. 3. Migration route of the only plaice in the current study to migrate into Scottish waters. The fish was released on 19/02/98 (cross), and the tag ceased recording on 30/09/98. Filled circles represent 14 locations recorded between these dates. Arrows indicate the probable migration route. No recapture position was returned with the fish, which was landed in Eyemouth in the Scottish Borders.

Northern and eastern subgroup plaice, which were separated geographically during the summer, mixed during winter on recognized spawning grounds in the German Bight in the eastern North Sea (Fig. 2, panels 3–7). Furthermore, representatives of all three subgroups were found on spawning grounds in the Southern Bight in the southern North Sea. The only fish during the current study to leave the North Sea were 13 plaice from the western subunit that entered the eastern English Channel to reach spawning grounds located immediately to the west of the Dover Strait (Fig. 2, panels 4 and 5). Recording ceased for seven of these individuals while on the spawning ground. Of the remaining six fish, four exhibited post-spawning migrations back into the south-western North Sea and two fish remained in the eastern English Channel during the following feeding season (Fig. 2, 1st panel).

Figure 4 illustrates the assumed spawning locations of 82 plaice that performed pre- and post-spawning migrations. For 96% of these fish, this was the southernmost limit of distribution. The assumed spawning distribution very closely matched the previously described distribution of plaice eggs (Harding, Nichols & Tungate 1978), as shown on the figure.

PHYSICAL CONDITIONS EXPERIENCED BY POPULATION SUBUNITS

Fish in the eastern and western subunits occupied depths of between 30 and 50 m (Fig. 5a) and experienced a seasonal rise and fall in ambient temperature,

between a winter minimum of 5·1 °C and a summer maximum of 17 °C (Fig. 5b). By contrast, the northern subunit spent the summer at 50–60 m depth, where the average temperature never rose above 9·5 °C. In winter, however, the northern subunit plaice migrated into shallower depths (40–50 m) to spawn.

Following the removal of geographical location as a factor, cluster analysis of the June data, based on depth and temperature, identified just two clusters (Fig. 6a). The northern subunit remained distinct; however, the temperature and depth characteristics experienced by the western and eastern subunits were not identified as separate groupings by the analysis. The same analysis on the January data (Fig. 6b) identified a minimum of five clusters, with heavily overlapping distributions.

We tested the independence of the January and June classifications by using a Fisher's exact test on the 30 individuals common to both data sets. We found no association between the group classification in January and the group classification in June ($P = 0·24$). This confirms that feeding aggregation membership and spawning location were not linked.

Discussion

To our knowledge, this is the first time that a geolocation-based field study has been able to demonstrate clear temporal subdivision of a free-ranging fish population into geographically discrete subunits. This subdivision occurred only during the non-breeding season; there was substantial mixing of individuals on the spawning grounds. Temperature and depth data recorded by the data storage tags suggest that the distribution pattern observed was related at least partially to seasonal thermal stratification of the North Sea. This feature of spatial dynamics has neither been predicted, nor is apparent from either historical tagging (Bolle *et al.* 2001) or genetically based investigations (Hoarau *et al.* 2002). Indeed, our results suggest that sampling on spawning grounds within the spawning season does not guarantee the genetic integrity of samples obtained.

DISTRIBUTION AND DISPERSION

The concept of plaice subpopulations is not new (De Veen 1978; Cushing 1990). However, where De Veen (1978) suggested aggregation onto spawning areas during winter followed by dispersion onto feeding grounds in summer, we identified three population subunits that diverged onto discrete feeding grounds in the northern part of their range during summer, then dispersed onto southerly spawning areas, where the fish mixed together during winter. This pattern is the opposite of the expected pattern of breeding-related seasonal dispersion and aggregation observed in migrating birds (Alerstam 1990; Berthold 2001).

No single physical factor stands out that can explain the divergent feeding aggregations. For example, they
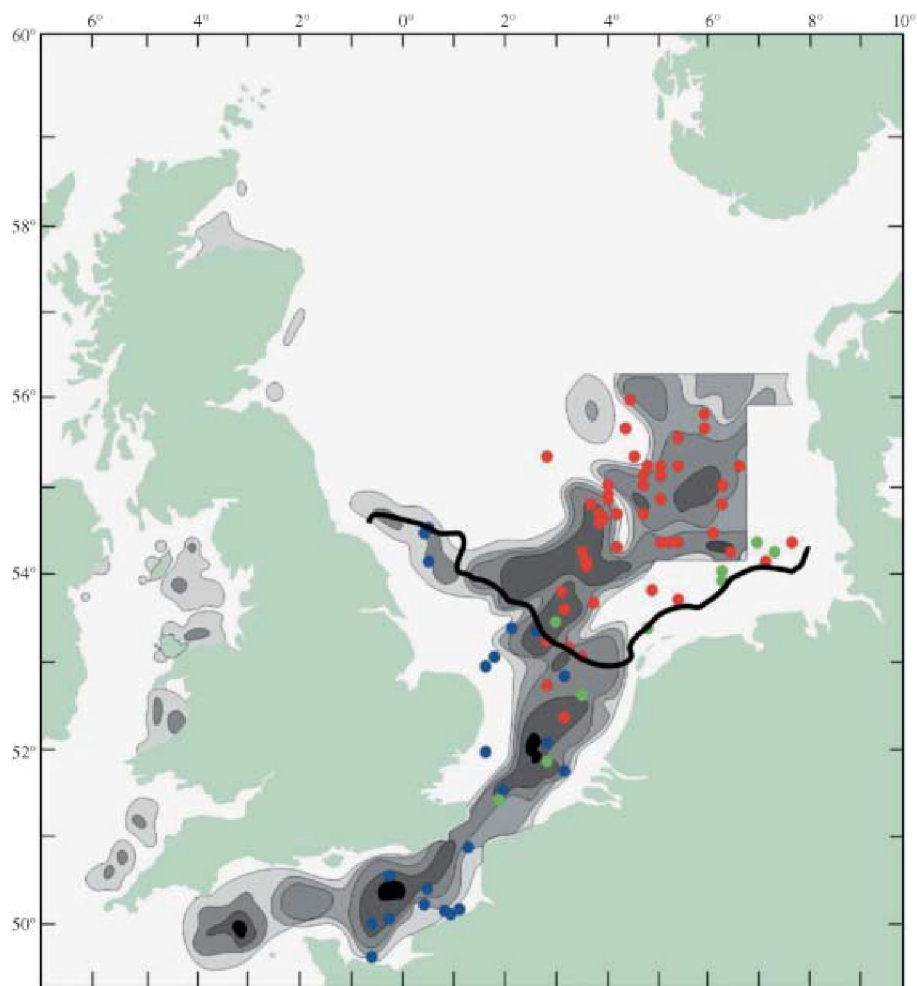
Fig. 4. Assumed spawning locations of 82 electronically tagged plaice (see text for details). Colours indicate feeding aggregation membership of each individual (see Fig. 2). Spawning locations are plotted over the distribution of plaice eggs, where dark colouration indicates the highest egg densities (modified from Harding *et al*. 1978). The thick black line indicates the 0·3 ms^{-1} average tidal current velocity contour (see Fig. 1).

cannot be explained solely by temperature (see below), because similar temperatures are found in areas where the fish occur at much lower densities. There are also no obvious physical features of these three areas that make them stand out from other parts of the central and northern North Sea. For example, the depths and bottom substrates are not unique to these areas (British Geological Survey 1991).

The level of dispersion observed during spawning was not due to differential timing of individual fish migrations, but due to the widespread geographical area that the plaice visited to spawn, irrespective of summer location. The use of southerly spawning grounds may be for several reasons. First, there may be a need for warmer water during maturation of gonads and early development of larvae (Lam 1983). Secondly, the tidal currents in the south will bring the larvae toward shallow coastal nursery areas (Harden Jones 1968; Cushing 1990). The specific roll of the tidal streams and their interaction with temperature in structuring the adult North Sea plaice population are considered below.

THE INFLUENCE OF TIDAL STREAMS ON SPATIAL DISTRIBUTION

Unlike the situation for most birds (Alerstam 1990), the environmental transport system or 'conveyor belt' available to plaice in the form of the tidal streams is relatively well defined, and several authors have suggested that plaice stocks are contained within the tidal streams (Harden Jones 1968; Arnold & Cook 1984; Cushing 1990). Our results illustrate that two of three population subunits (feeding aggregations) were indeed located at the branch terminals of the tidal streams, but the third (northern) subunit lays outside of the influence of the transport system. Northern fish often travelled in excess of 250 km to spawn, without the benefit of tidal transport. It should be noted that because we did not tag fish off the north-east coast of England during the spawning season, our results may mask the existence of a fourth population subunit off the Scottish coast, where plaice are also known to occur (De Veen 1978; Lockwood & Lucassen 1984).
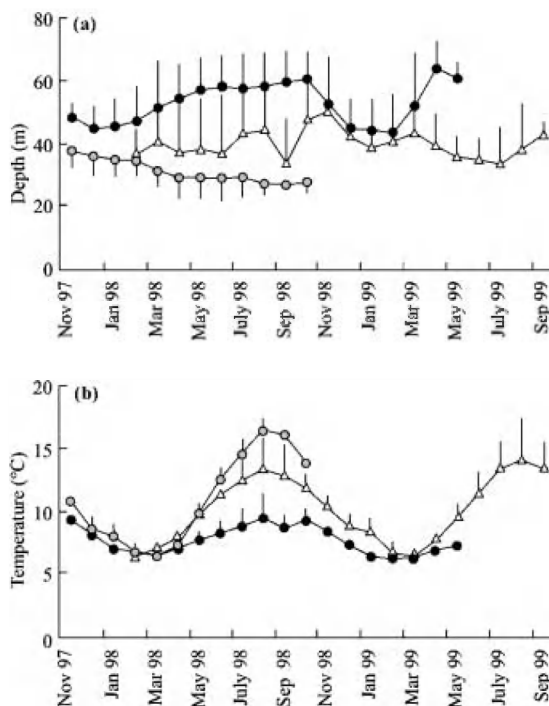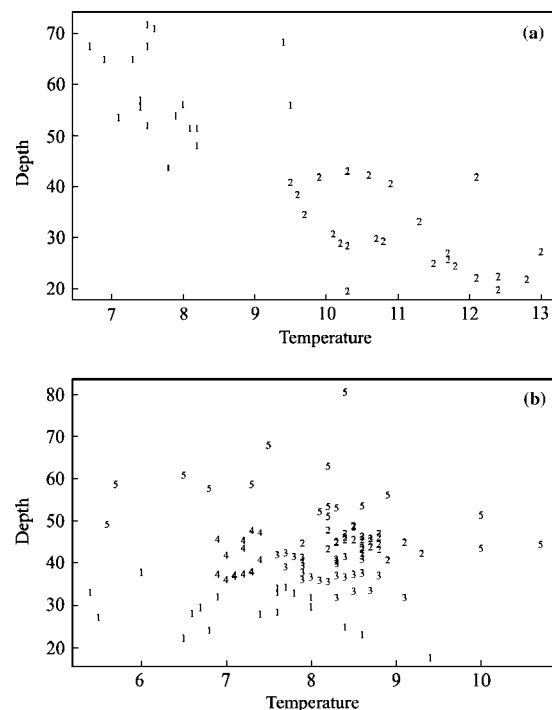
Fig. 5. Average monthly (a) sea-bed depth and (b) temperature, experienced by plaice carrying electronic data storage tags. Open squares = western subunit; grey = eastern subunit; black = northern subunit.

Fig. 6. Cluster analysis of the plaice distribution in (a) June and (b) January, based on depth and temperature. Labels indicate group membership.

The majority of the northern plaice did not move south of the 0·3 ms⁻¹ average tidal current velocity contour (Fig. 4). Their migration occurred along an approximate north–south axis, at right angles to the primary axis of tidal flow (Harden Jones *et al*. 1979). These factors all suggest that it is unlikely that tidal stream transport contributed to the migrations of the majority of these fish (Weihs 1978; Metcalfe *et al*. 1990). We also observed (unpublished data) that a few plaice from each of the subunits were capable of entering, leaving and sometimes crossing the tidal stream paths. This suggests that although tidal streams may provide directional clues (Harden Jones 1984; Gibson 1997), a significant navigational component involving external cues may also be involved (Metcalfe, Holford & Arnold 1993), and that the containment of tidally transporting fish is not absolute.

THE INFLUENCE OF TEMPERATURE ON SPATIAL DISTRIBUTION

Our results show that during the summer feeding period, the northern subunit was separated from the eastern and western subunits by the North Sea thermal front, the southern boundary of the area of seasonal thermal stratification (Pingree & Griffiths 1978). The location of the front itself is determined by the strength of the tidal stream currents. The stronger currents in the southern North Sea prevent the establishment of a stratified surface layer of warm water.

The eastern and western subunits remained in warm, thermally mixed water south of the front, whereas the northern subunit was located in deeper, cold, thermally stratified water. The thermal front represented a distributional limit for each of the subunits, and appeared to represent a physical barrier to the northward movement of warm-adapted plaice. Western and eastern subunit plaice rarely occurred in water deeper than 40 m (Fig. 5), the approximate depth of the thermally stratified layer (Pingree & Griffiths 1978; Brown *et al*. 1999). By contrast, the northern subunit plaice migrated through the thermal front before the winter breakdown of stratification, at the onset of the prespawning migration (Hunter, Metcalfe & Reynolds, 2003b).

The association of fish with the areas bordering thermally stratified areas may also have foraging implications, given that temporally these are relatively stable features (Pingree & Griffiths 1978; Brown *et al*. 1999). There is a significant relationship between increased levels of primary productivity along thermal fronts (Pingree, Holligan & Mardell 1978; Riegman, Malschaert & Colijn 1990; Heilmann, Richardson & Aertebjerg 1994) and increased productivity at higher levels in the food chain (Lindley & Williams 1994; Josefson & Conley 1997; Skov & Durinck 1998). Although corroborative data are not available, it seems reasonable to assume that increased primary productivity in the water column would result in seasonally predictable increased food resources on the sea-bed (Barry & Dayton 1991).

Conclusions

Our results support the hypothesis that variation in migratory behaviour of North Sea plaice may be due to large-scale differences in the speed and directions of the tidal streams. The tidal streams provide transport and guidance for migration in fast-flowing areas, and also influence summer distribution limits by controlling the extent of thermal stratification in the North Sea. Our discovery that the fish split into discrete subpopulations during the non-breeding season, followed by mingling of subunits during spawning, was the opposite of the typical pattern exhibited by migrating birds. We cannot determine the extent of this type of behaviour in migrating fish; however, conventional tagging has also suggested that a similar pattern may be exhibited by adult bass, *Dicentrarchus labrax* L. (Pawson, Kelley & Pickett 1987).

Our results from 145 individuals tagged with electronic data storage tags have revealed features of migratory behaviour not observed previously from a century of conventional tagging experiments. Furthermore, the ability to link spatial distribution to physical characteristics of the marine environment should improve our ability to predict how natural and anthropogenic perturbations may affect the future distributions of these fish. For example, the implementation of closed areas in the North Sea as a conservation measure (European Commission 2001) will succeed only if the protected areas are circumscribed with consideration of the seasonal movements and spatial distribution of the fishes to be protected (Horwood *et al.* 1998; Metcalfe *et al.* 1999).

Acknowledgements

References

Alerstam, T. (1990) *Bird Migration*. Cambridge University Press, Cambridge.

Arnold, G.P. & Cook, P. (1984) Fish migration by selective tidal stream transport: first results with a computer simulation model for the European continental shelf. *Mechanisms of Migration in Fishes* (eds J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill), pp. 227–261. Plenum Press, New York.

Arnold, G.P. & Dewar, H. (2001) Electronic tags in marine fisheries research: a 30 year perspective. *Electronic Tagging and Tracking in Marine Fisheries* (eds J.R. Sibert & J.L. Nielsen), pp. 7–64. Kluwer Academic Press, Dordrecht, the Netherlands.

Barry, J.P. & Dayton, P.K. (1991) Physical heterogeneity and the organization of marine communities. *Ecological Heterogeneity* (eds J. Kolasa & S.T.A. Pickett), Ecological Studies vol. 86, pp. 270–320. Springer Verlag, New York.

Ben-Tuvia, A. (1995) Biological characteristics of middle-sized pelagic fishes. *International Symposium on Middle-Sized Pelagic Fish* (eds C. Bas, J.J. Castro & J.M. Lorenzo), pp. 205–209. Scientia Marina, Barcelona.

Berthold, P. (2001) *Bird Migration: A General Survey*, 2nd edn. Oxford University Press, Oxford.

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., . Boustany, A., Teo, S.L.H., Seitz, A., Walli, A. & Fudge, D. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*, **293**, 1310–1314.

Bolle, L.J., Hunter, E., Rijnsdorp, A.D., Pastoors, M.A., Metcalfe, J.D. & Reynolds, J.D. (2001) *Do Tagging Experiments Tell the Truth? Using Electronic Tags to Evaluate Conventional Tagging Data*. ICES CM 2001/O: 02. International Council for the Exploration of the Sea, Copenhagen.

Boustany, A.M., Davis, S.F., Pyle, P., Anderson, S.D., Le Boeuf, B.J. & Block, B.A. (2002) Expanded niche for white sharks. *Nature*, **415**, 35–36.

British Geological Survey (1991) *Geology of the United Kingdom, Ireland and the Adjacent Continental Shelf. 1: 1 000 000 Scale*. British Geological Survey, Keyworth.

Brown, J., Hill, A.E., Fernand, L. & Horsburgh, K.J. (1999) Observations of a seasonal jet-like circulation at the central North Sea cold pool margin. *Estuarine, Coastal and Shelf Science*, **48**, 343–355.

Cushing, D.H. (1990) Hydrographic containment of a spawning group of plaice in the. Southern Bight of the North Sea. *Marine Ecology Progress in Series*, **58**, 287–297.

De Veen, J.F. (1978) On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. *Netherlands Journal of Sea Research*, **12**, 115–147.

European Commission (2001) Commission Regulation EC no. 259/2001. *Official Journal*, Vol. L, 39/7.

Gibson, R.N. (1997) Behaviour and distribution of flatfishes. *Journal of Sea Research*, **37**, 241–256.

Greer Walker, M., Harden Jones, F.R. & Arnold, G.P. (1978) The movements of plaice (*Pleuronectes platessa* L.) tracked in the open sea. *Journal du Conseil International pour l'Exploration de la Mer*, **38**, 58–86.

Harden Jones, F.R. (1968) *Fish Migration*. Edward Arnold Ltd, London.

Harden Jones, F.R. (1984) Could fish use inertial cues when on migration? *Mechanisms of Migration in Fishes* (eds J.D. McCleave, G.P. Arnold, J.J. Dodson & W.H. Neill), pp. 67–78. Plenum Press, New York.

Harden Jones, F.R., Arnold, G.P., Greer Walker, M. & Scholes, P. (1979) Selective tidal stream transport and the migration of plaice (*Pleuronectes platessa* L.) in the southern North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, **38**, 331–337.

Harding, D., Nichols, J.H. & Tungate, D.S. (1978) The spawning of plaice (*Pleuronectes platessa* L.) in the Southern Bight. *Rapports et Proces-Verbaux des Reunion – CIESM*, **172**, 102–113.

Heilmann, J., Richardson, K. & Aertebjerg, G. (1994) Annual distribution and activity of phytoplankton in the Skager-rack/Kattegat frontal region. *Marine Ecology Progress in Series*, **112**, 213–223.

Hilborn, R. (1990) Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Science*, **47**, 635–643.

Hoarau, G., Rijnsdorp, A.D., Van der Veer, H.W., Stam, W.T. & Olsen, J.L. (2002) Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large scale spatial and temporal homogeneity. *Molecular Ecology*, **11**, 1165–1176.

Horwood, J., Nichols, J. & Milligan, S. (1998) Evaluation of closed areas for fisheries management. *Journal of Applied Ecology*, **35**, 893–903.

Hunter, E., Aldridge, J.N., Metcalfe, J.D. & Arnold, G.P. (2003a) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. I. Tidal location method. *Marine Biology*, **142**, 601–609.

Hunter, E., Metcalfe, J.D., Holford, B.H. & Arnold, G.P. (2004) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. II. Reconstruction of plaice ground-tracks. *Marine Biology*, in press.

Hunter, E., Metcalfe, J.D. & Reynolds, J.D. (2003b) Migration route and spawning site fidelity by North Sea plaice. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **270**, 2097–2103.

Josefson, A.B. & Conley, D.J. (1997) Benthic response to a pelagic front. *Marine Ecology Progress in Series*, **147**, 49–62.

Lam, T.J. (1983) Environmental influences on gonadal activity in fish. *Fish Physiology* (eds W.S. Hoar, D.J. Randall & E.M. Donaldsen), pp. 65–116. Academic Press, London.

Lindley, J.A. & Williams, R. (1994) Relating plankton assemblages to environmental variables using instruments towed by ships-of-opportunity. *Marine Ecology Progress in Series*, **107**, 245–262.

Lockwood, S.J. & Lucassen, W. (1984) The recruitment of juvenile plaice (*Pleuronectes platessa* L.) to their parent spawning stock. *Journal du Conseil International pour l'Exploration de la Mer*, 41, 181–193.

Loewe, P. (1998) Surface temperatures of the North Sea in 1997. *Deutsche Hydrographische Zeitschrift*, **50**, 71–80.

Metcalfe, J.D. & Arnold, G.P. (1997) Tracking fish with electronic tags. *Nature*, **387**, 665–666.

Metcalfe, J.D., Arnold, G.P. & McDowall, P.W. (2002) *Migration Handbook of Fish Biology and Fisheries*, Vol. 1 *Fish Biology* (eds P.J.B. Hart & J.D. Reynolds), pp. 175–199. Blackwell Publishing, Oxford.

Metcalfe, J.D., Arnold, G.P. & Webb, P.W. (1990) The energetics of migration by selective tidal stream transport: an analysis for plaice tracked in the southern North Sea. *Journal of the Marine Biology Association of the UK*, **70**, 149–162.

Metcalfe, J.D., Holford, B.H. & Arnold, G.P. (1993) Orientation of plaice (*Pleuronectes platessa*) in the open sea: evidence for the use of external directional clues. *Marine Biology*, **117**, 559–566.

Metcalfe, J.D., Hunter, E., Holford, B.H. & Arnold, G.P. (1999) *The Application of Electronic Data Storage Tags to Spatial Dynamics of Fish Populations*. ICES CM. 1999/AA: 1. International Council for the Exploration of the Sea, Copenhagen.

Novikov, Y.V. (1986) Some trends of distribution and migration of common pelagic fishes of the north-western Pacific Ocean. *Journal of Ichthyology*, **26**, 161–172.

Pawson, M.G., Kelley, D.F. & Pickett, G.D. (1987) The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. *Journal of the Marine Biology Association of the UK*, **67**, 183–217.

Pingree, R.D. & Griffiths, D.K. (1978) Tidal fronts on the shelf seas around the. *British Isles Journal of Geophysical Research*, **83**, 4615–4622.

Pingree, R.D., Holligan, P.M. & Mardell, G.T. (1978) The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. *Deep Sea Research*, **25**, 1011–1028.

Riegman, R., Malschaert, H. & Colijn, F. (1990) Primary production of phytoplankton at a frontal zone located at the northern slope of Dogger Bank (North Sea). *Marine Biology*, **105**, 329–336.

Rijnsdorp, A.D. & Pastoors, M.A. (1995) Modelling the spatial dynamics and fisheries of North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. *ICES Journal of Marine Science*, **52**, 963–980.

Skov, H. & Durinck, J. (1998) Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrack. *Journal of Sea Research*, **39**, 305–311.

Weihs, D. (1978) Tidal stream transport as an efficient method for migration. *Journal du Conseil International pour l'Exploration de la Mer*, **38**, 92–99.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clarke, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The Migration Atlas: Movements of the Birds of Britain and Ireland*. T. & A.D. Poyser, London.