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REVIEW OF MIGRATORY ROUTES AND BEHAVIOUR OF ATLANTIC SALMON, SEA TROUT AND EUROPEAN EEL IN SCOTLAND'S COASTAL ENVIRONMENT: IMPLICATIONS FOR THE DEVELOPMENT OF MARINE RENEWABLES

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Contents

Executive Summary 1

1.0 Introduction 2

2.0 Atlantic salmon (*Salmo salar*) 2
- 2.1 Salmon post-smolt migration 5
- 2.2 Salmon post-smolt migratory behaviour 6
- 2.3 Salmon migration in distant waters 7
- 2.4 Coastal migration routes for adult salmon 12
- 2.5 Adult salmon migratory behaviour 31
- 2.6 Salmon kelts 32

3.0 Anadromous Brown Trout (*Salmon trutta*) 34
- 3.1 Post-smolt migration and behaviour of sea trout 35
- 3.2 Marine migration of sea trout adults 37

4.0 European Eel (*Anguilla anguilla*) 41
- 4.1 Juvenile eel - migration routes 43
- 4.2 Juvenile eel - migration timing 47
- 4.3 Juvenile eel - migration behaviour 48
- 4.4 Adult eel - migration routes 48
- 4.5 Adult eel - migration timing 50
- 4.6 Adult eel - migration behaviour 51

5.0 Summary 53
- 5.1 Salmon 53
- 5.2 Sea trout 55
- 5.3 European eel 56

6.0 Knowledge Gaps 57
- 6.1 Salmon 57
- 6.2 Sea trout 58
- 6.3 European eel 58

7.0 Conclusions 59

8.0 Acknowledgements 59

9.0 References 60

Figures and Tables

Figure 1 Map showing the distribution of salmon in Scottish rivers. Updated from the original salmon distribution map of Gardiner and Egglishaw (1985).

Figure 2 Map showing the distribution of Special Areas of Conservation (SACs) for Atlantic salmon in Scotland.

Figure 3 Map of North Atlantic area showing dominant ocean currents

Figure 4 Temporal variability in reported catches from the Faroes, East and West Greenland together with the proportion of fish recaptured from Carlin tagging programmes at the Girnock Burn, Deeside.

Figure 5 The coastal movement of salmon caught in the North east England drift net fishery (after Potter and Swain, 1982).

Figure 6 Map showing the distribution of coastal recaptures of fish tagged at Rockhall, 5 miles to the North of Montrose (after Shearer, 1958).

Figure 7 Map showing the distribution of coastal recaptures of fish tagged on the Black Isle 1913-14 (after Calderwood, 1914).

Figure 8 Map showing the distribution of coastal recaptures of fish tagged on the coast of Sutherland in 1915 (after Calderwood, 1915).

Figure 9 Map showing the distribution of recaptures of fish tagged in Thurso Bay (1920) (after Calderwood, 1920).

Figure 10 Map showing the distribution of recaptures of fish tagged at Loch Inchard (1936) (after Menzies, 1937).

Figure 11 Map showing the distribution of recaptures of fish tagged at Raffin (1937) (after Menzies, 1938a).

Figure 12 Map showing the distribution of recaptures of fish tagged at Soay and Fascadale (1938) (after Menzies, 1938b)

Figure 13 Map showing the distribution of recaptures of 1SW (grilse) tagged in the Girnock Burn as smolts (1968-81).

Figure 14 Map showing the distribution of recaptures of MSW (salmon) tagged in the Girnock Burn as smolts (1968-81).

Figure 15 Map showing the distribution of recaptures of salmon (including grilse) tagged in the River Tay (Almond and Tummel) as smolts (1967-88).

Figure 16 Map showing the distribution of salmon marked as smolts in the North Esk and subsequently recaptured.

Figure 17 Map showing the distribution of net fisheries in Scotland in 2008.

Figure 18 Map showing the distribution of sea trout recapture locations from tagging programmes in the rivers North Esk, South Esk and Bervie.

Figure 19 Map showing the distribution of sea trout recapture locations from a compilation of tagging programmes on the River Tweed (Ronald Campbell, pers. comm.).

Figure 20 Eel presence or absence for sites electrofished in Scotland RBD between 1996 and 2006.

Figure 21 Percentage frequency of eel abundance class at electrofishing sites in various rivers or districts of Scotland RBD

Figure 22 Ocean currents in the vicinity of the British Isles. Background image ©2010 Google - Imagery ©2010 TerraMetrics, NASA

Figure 23 Dominant directions of travel for Atlantic salmon (1SW and MSW) in Scottish coastal waters based on tagging studies

Figure 24 Summary of the movements of silver eels observed in specific tracking studies.

Table 1 Summary statistics showing the percentage and annual variability of repeat spawners in the net and coble fishery of the rivers Dee, North Esk, Spey, Tay and Tweed together with the number of sampling years and sample sizes (Phil Bacon, pers. comm.).

Review of migratory routes and behaviour of Atlantic salmon, sea trout and European eel in Scotland's coastal environment: implications for the development of marine renewables

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Executive Summary

The Scottish Government has ambitious targets for renewable energy production, to which offshore renewables could make a substantial contribution. However, the new marine energy industries must develop on a sustainable basis, ensuring that environmental impacts are assessed, and if necessary, minimised through appropriate mitigation. The likelihood of any impacts on Atlantic salmon, sea trout or European eels will depend on interactions between (1) migratory routes and behaviour (2) the distribution of offshore developments (3) the technologies deployed and (4) the dynamics of the relevant fish populations. This report summarises available information on the migratory routes and behaviour of salmon, sea trout and eels in a Scottish context.

Broad scale patterns of migration are identified for adult Atlantic salmon, although the resolution of available data is unlikely to be sufficient to inform site specific risk assessment. Less extensive information is available on juvenile migratory routes and no information is available on juvenile migration from important east coast rivers. The limited information available on sea trout migration suggests predominantly inshore and local use of the marine environment, although wider ranging migrations have been observed from some rivers. No specific migratory routes can be discerned for either juvenile or adult sea trout. European eels in Scotland are part of a single European population for which there is considerable uncertainty regarding migratory routes. The limited evidence which is available suggests that eels from a number of European countries may migrate through Scottish waters. For all the species considered, there is only very limited information on behaviour and swimming depths. Most of this information has been generated outwith Scotland and it is uncertain whether it can be reliably transferred to the Scottish context given differences in the life stages observed and local geography.

Significant knowledge gaps remain for all three species considered in this review. These knowledge gaps should be considered as part of an overall assessment of research needs in relation to offshore renewable developments and diadromous fish.

1.0 Introduction

The Scottish Government has set ambitious targets to generate 80% of national power capacity from renewable sources by 2020. As part of this initiative it is increasingly desirable in policy terms to develop Scotland's coastal seas for power generation. However, there is also a need to assess, manage and minimise environmental impacts of offshore renewable projects through planning and licensing processes. One area of importance is the potential of offshore renewable projects to impact on migratory fish populations including Atlantic salmon, sea trout and European eel. These species are of particular concern due to their high economic and/or conservation value, broad geographic distribution and extensive marine migration through Scottish coastal waters.

The potential impact of offshore renewable energy developments on migratory fish populations will depend on the interactions between (1) the spatial distribution and behaviour of fish in the coastal environment; (2) the spatial distribution of specific offshore renewable technologies; and (3) the average effect of particular renewable technologies on individual fish and subsequently the populations to which they belong. This review is concerned with identifying and summarising information in relation to the first of these factors.

This review summarises available information regarding the migratory routes used by Atlantic salmon, sea trout and European eel in Scottish coastal waters. The review includes broader European, North American and Japanese studies where these provide additional insights into migratory behaviour. The report is structured by species, life stage, migratory routes and behaviour. Based on an assessment of available data and the offshore development context, an assessment of knowledge gaps and requirements is made, together with recommendations.

2.0 Atlantic Salmon (*Salmo salar*)

The Atlantic salmon is widely distributed in Scotland (Fig. 1) and its populations are recognised as being of both national and international importance. Based on data collected between 2003 and 2007, catches of Scottish salmon account for 60% and 12% of the UK and European nominal catch (fish killed and retained), respectively

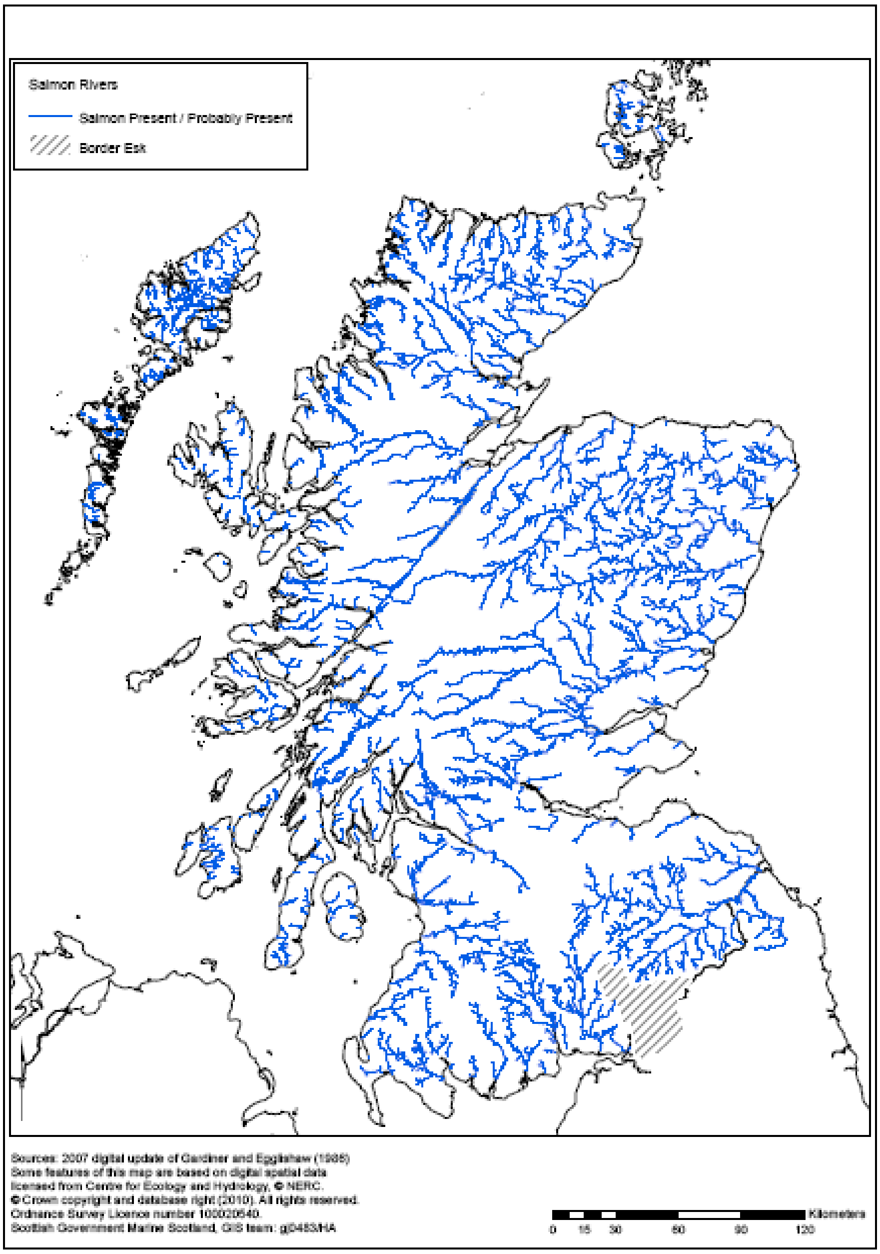

Figure 1 Map showing the distribution of salmon in Scottish rivers. Updated from the original salmon distribution map of Gardiner and Egglishaw (1985).

(ICES, 2009). If 'catch and release' is also considered then this is likely to be a conservative estimate of the relative importance of Scottish rivers given that this practice has been widespread in recent years. In recognition of the European importance of Scotland's salmon populations 11 rivers are designated as Special Areas of Conservation (SACs) for Atlantic salmon and they are a qualifying feature at an additional six sites (Fig. 2).

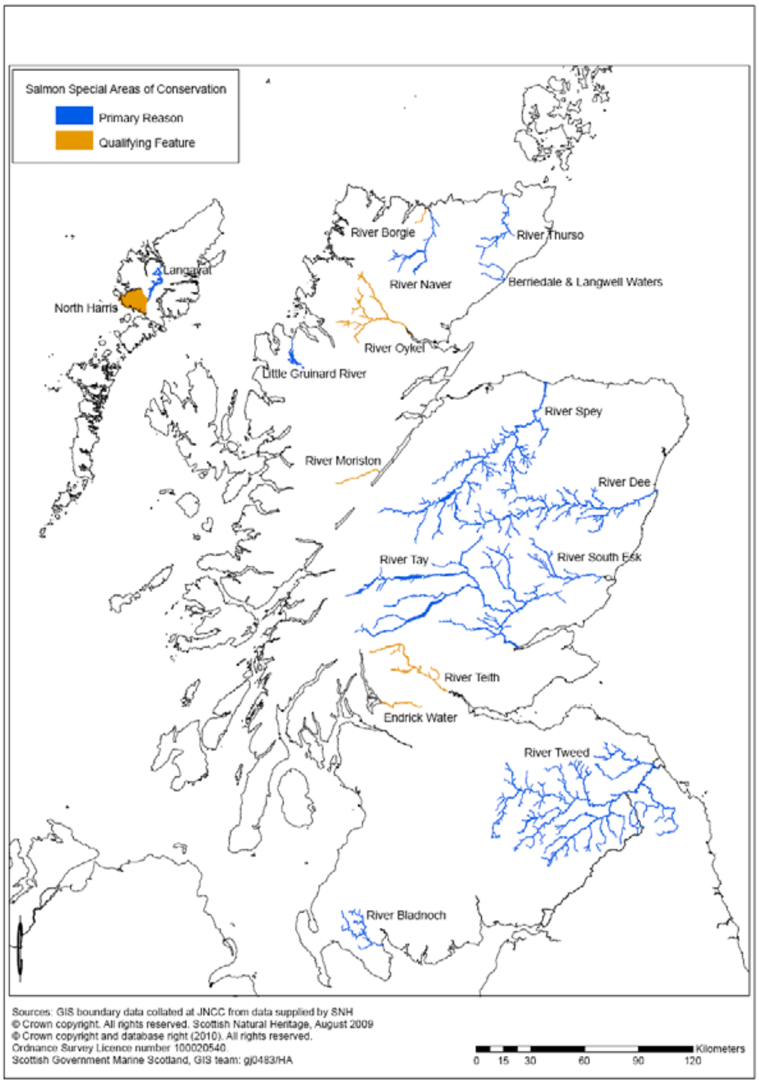

Figure 2 Map showing the distribution of Special Areas of Conservation (SACs) for Atlantic salmon in Scotland.

The juvenile life stage of salmon takes place in fresh water and typically lasts for between 1 and 4 years before surviving fish migrate to sea as smolts. Following entry to the sea, the fish are known as post-smolts until the spring of the following year. Atlantic salmon grow rapidly by feeding in the ocean but return (or "home") to their native rivers to spawn. There are distinct components to the homeward migration (Hansen *et al.,* 1993). The first oceanic phase is rapid and highly directed, probably involving navigation or orientation using position of sun and reference to the Earth's magnetic field (Hansen & Quinn, 1998). The final phases of up-river migration are thought to use the sense of smell to detect olfactory cues that are remembered from the outward migration (Hasler & Scholz, 1983). Very little is understood of the phase of migration between location by salmon of the home land-mass and identification of the home river.

Fish that have spent a single winter at sea before returning are known as grilse or 1 sea-winter (1SW) fish. Fish that have spent more than one winter at sea (typically after 2, but up to 5 winters) are known as salmon or multi-sea-winter (MSW) fish, although their exact age may also be specified - for example, as two sea winter (2SW).

2.1 Salmon Post-Smolt Migration

There is little systematic information on the routes used by Atlantic salmon to migrate from Scotland to their distant ocean feeding grounds (Shearer, 1992). Sea surface trawls have provided the majority of the information that is available (Holm *et al.,* 2000).

Sea surface trawls, primarily conducted by Norwegian scientists (Holm *et al.,* 2000; Hanson, *et al.,* 2002), but also including more limited efforts by UK researchers (Shelton *et al.,* 1996, 1997) show that some post-smolts of unknown river origin migrate northwards off the western coast of Scotland along the continental shelf edge, apparently making use of the dominant ocean currents. More generally, high densities of post-smolts are reported to the north and northwest of Scotland in a highly dispersed pattern of distribution throughout much of the Norwegian Sea (Holm *et al.,* 2000).

More recently the EU SALSEA–Merge project, which aims to improve understanding of salmon migration and distribution, has attempted to supplement traditional trawls with genetic identification of post-smolts to identify the river of origin. Samples of post-smolts have been obtained from sea surface trawls off the west and north of Scotland and Ireland confirming the presence of post-smolts (URL 1) as identified by previous studies. At present the information on region origin is not available, but it is due for delivery in 2010. This should provide additional insights into migratory routes associated with particular river systems although its relevance in the current context is conditional on the sampling strategy adopted, the time of sampling, and the locations in the ocean where post-smolts have been obtained.

Salmon post-smolts originating from Scottish rivers inevitably use near-shore areas at the commencement of the marine migration. However, based on currently available information it is not possible to describe how migratory routes vary with river of origin or to define the duration or extent of their initial dependence on near- and off-shore areas. In particular, there is a notable lack of knowledge on the use of routes in the North Sea by post-smolts leaving the dominant salmon rivers of eastern Scotland. Sampling of the likely relevant areas was not included in the SALSEA-Merge initiative. Accordingly, as matters stand, there is limited information available on the major migratory routes of salmon post-smolts leaving Scottish rivers and the subject area remains poorly understood.

2.2 Salmon Post-Smolts - Migratory Behaviour

Although there have been no substantive studies on the migratory behaviour of salmon post-smolts in the Scottish marine environment, tagging studies conducted in Canada and Norway provide some general insights, especially in relation to speed and depth of migration and habitat use during migration.

The studies conducted in Norway have focussed on post-smolt migrations within fjords rather than in the open sea. This has allowed researchers to work in a spatially constrained environment where manual tracking or acoustic receivers provide the opportunity to track the movements of acoustically tagged post-smolts. Thorstad *et al.* (2004) tracked four hatchery-reared smolts in a fjord leading from the River Eira; the fish travelled rapidly and actively towards the open sea (mean net seaward movement of 510 metres per hour) but with frequent directional changes. It was concluded that fish movement was independent of tidal currents and that fish did not use currents as orientation cues, although the least frequent direction of travel was back towards the river. The post-smolts did not appear to use the immediate near-shore areas, with the mean distance to shore reported at 370m.

Finstad *et al.* (2005) conducted a second, similar experiment at the Eira site, tagging 25 hatchery-reared salmon smolts. Migration was monitored using curtains of acoustic receivers at distances of 9, 32, 48 and 77km from the release location at the mouth of the River Eira. Post-smolts spent more time travelling through the inner fjord than further out. As in the previous study, they were observed to move rapidly being recorded at 9, 48 and 77km from the river in average times of 28, 65 and 83 hours, respectively. There did not appear to be a standard migratory route through the fjord because fish were detected at a range of locations along the curtain of receivers.

Thorstad *et al.,* (2007) also investigated potential differences in migratory behaviour of hatchery-reared and wild salmon smolts, also at the Eira. The study of wild fish was made possible by developments in tagging technology that permitted the use of smaller acoustic tags on wild salmon smolts. Receivers were located at 9.5, 37 and 65km from the release point. The study did not find any difference in the rate of travel of wild or hatchery fish when the effect of body length was standardised. Salmon were again found to utilise the full width of the fjord and to travel rapidly.

Similar observations of rapid, active migration have also been reported in eastern Canada. Lacroix *et al.* (2005) investigated the early marine migration of 55 wild and hatchery reared Atlantic salmon post-smolts in the Bay of Fundy on the east coast of Canada using curtains of acoustic receivers at distances of 5-10km and 20km. Seventy-one per cent of post-smolts travelled as far as the 5-10km receiver array within 12 hours and 94% did so within 24 hours. Fish tended to travel near to the coast, 2.5-5km from shore. Once smolts had passed the 5-10km receivers, two distinct behavioural patterns were observed. Some fish left the bay directly, while others remained within the bay moving back and forth over several days. Fish were found to be strongly influenced by tidal direction in their movements and this potentially also influenced their spatial distribution.

None of the above studies provide information on swimming depths. Davidsen *et al.* (2008) manually tracked eight hatchery reared Atlantic salmon post-smolts, again in a fjord in Norway, this time using implanted acoustic depth-sensing transmitters. The fish were tracked for between 5 and 12 hours. Recorded swimming depths ranged between 0 and 6.5m while the percentage of time spent between 1 and 3m ranged from 49-99% during daylight for all fish. There were large variations in the swimming depths of individuals; four of the smolts swam closer to the surface when light levels were lower, being found at <0.5m depth during night time, while three of the smolts remained at 2-3m throughout tracking. In similar work by Plantalech Manel-La *et al.* (2009), eight hatchery-reared salmon smolts were tagged with depth sensitive acoustic tags. The study was conducted in the Hardangerfjord system in Norway using manual tracking procedures. The fish did not migrate directly out of the fjord. Mean migration efficiency, calculated as the direct distance divided by the travelled distance, was 39%. The mean swimming depth was 1.7m although fish made regular vertical movements. The greatest measured swimming depth was 5.6m, despite a mean fjord depth of 150m and maximum depth of 800m. Swimming depth did not appear to relate to salinity, but may have been associated with water temperature since post-smolts appeared to use the warmer surface layers.

Given the lack of data from studies of post-smolt migrations in the UK generally and Scotland more specifically, it is difficult to predict the likely behaviour of salmon post-smolts in Scottish coastal waters. In general, the geography of Scottish coastal waters differs substantially from the locations examined in Norway and Canada. This is especially true for the major east coast rivers where there are no substantial bays or sea lochs (fjords). However, it is possible to identify some common findings across studies. Post-smolts were always observed to migrate rapidly and actively towards open marine areas after leaving their source rivers. They did not appear to closely follow nearby shores, although this may occur where coastal currents are substantial in this area. For the few studies where swimming depth was reported, it appears that post-smolts generally utilise shallow depths (typically 1-3m, but up to 6m). This latter observation is consistent with the effectiveness of sea surface trawls in catching post-smolts.

2.3 Salmon Migration in Distant Waters

The use of the marine environment by sub-adult and adult salmon outside Scottish waters is of interest because it may provide some indication as to the direction and routes used on return. Again, however, it should be noted that available information is relatively scarce and based largely on tagging studies from only two major fisheries

- in Greenland (primarily West Greenland) and the Faroes. These fisheries provide only limited geographical coverage of a potentially much wider area of marine distribution in the North Atlantic area (Fig. 3). It should also be noted that the West Greenland and Faroes fisheries operated with different intensities over different time scales (Fig. 4), with different seasonal deployment of effort and catch success. On this basis, care is required when making inferences based on recaptures of tagged fish. Finally, it is worth noting that despite considerable fisheries off the coast of Norway, no Scottish salmon tags are known to have been returned from the eastern Atlantic coasts (Hansen and Youngson, 2010). Consequently it seems likely that that this area is not used by Scottish adult salmon to any great extent and that eastward distribution of Scottish salmon is limited.

Figure 3 Map of North Atlantic area showing dominant ocean currents. Background image ©2010 Google - Imagery ©2010 TerraMetrics, NASA.

The catch of the Greenland fishery is dominated (>90%) by salmon destined to be MSW fish on return to their river of origin (Gauthier-Ouellet *et al.,* 2009). Much of the work reported from Greenland has been focussed at a coarse spatial resolution, separating North American and European stocks using discriminant analysis of scale growth patterns (Reddin *et al.,* 1988; Reddin and Friedland, 1999) or genetic assignment. In the latter case, finer geographical resolution is provided for North America (Sheehan *et al.,* 2009; Gauthier-Ouellet *et al.,* 2009). The relative contribution of North American fish to the West Greenland fishery is estimated to have varied between ca. 34% (1971) and 75% (1990) (Reddin and Friedland, 1999).

More detailed information on the origin of European salmon at West Greenland is available from tagging studies. ICES (2009) summarised the readily available data and provided a summary of the outcome of a major tagging programme conducted in

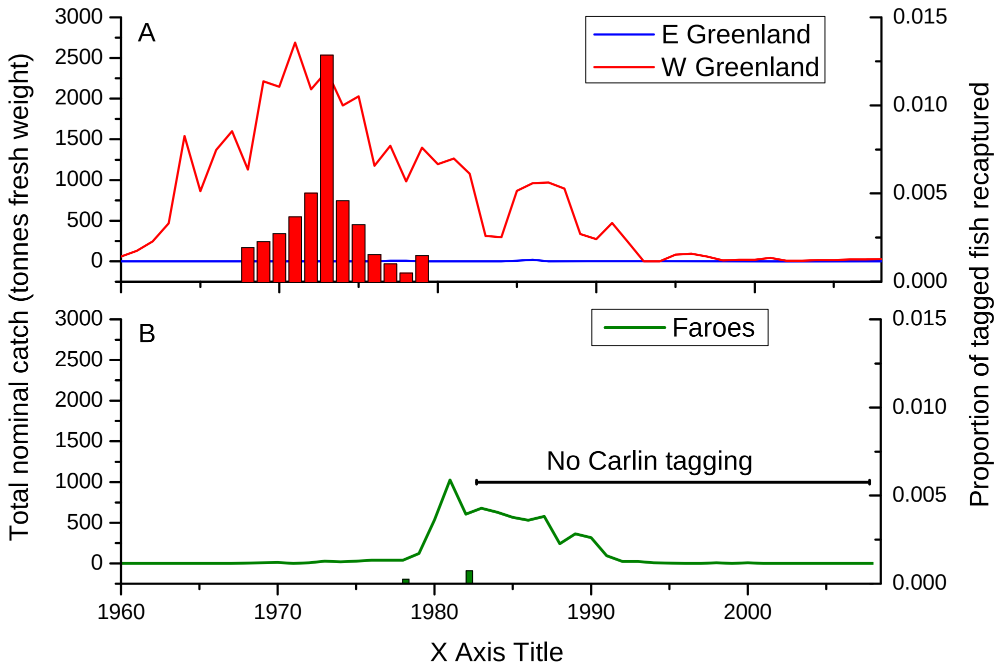

Figure 4. Temporal variability in reported catches (lines) and proportion of Girnock tagged fish caught in East and West Greenland (A) and the Faroes (B). The data indicates that for a given level of catch the Greenland and Faroes fisheries capture a similar number of Girnock fish, indicating that these fish use both locations. No fish recaptures were obtained after 1982 when Carlin tagging ceased. .

West Greenland between 1965 and 1972, based on subsequent tag recoveries in home waters. Of 4567 fish tagged, 30 were re-caught in Scotland. Although this figure is small, it is noteworthy that it was greater than for any of the other reporting countries. Consequently, Moller Jenson (1986) concluded that Canada and Scotland were the major contributors to catches in West Greenland.

The concept that fish from Scotland use the area around West Greenland is supported by recapture data from smolts tagged in Scottish rivers (Dee, Tay and North Esk). Much of these data are not available in an electronic format and as such analysis is difficult. However, data from the Girnock Burn, a small 30km^2 tributary catchment of the Aberdeenshire Dee, shows a substantial number of recaptures in West Greenland between 1968 and 1982 (Fig. 4). Near the peak of the fishery in 1973, 57 fish that had been tagged as smolts leaving the Girnock Burn were caught at West Greenland. Taken together, the adult tagging data from Greenland and the smolt tagging data from Scotland indicate that at least some Scottish MSW salmon make use of the extreme north-western Atlantic area.

Data from East Greenland and the Irminger Sea are sparse compared with those for West Greenland, probably reflecting the low effort from fisheries in this area and the low nominal catch (Fig. 2). Based on tag recapture data, ICES (2009) suggested that the East Greenland fishery tended to exploit fish of northern European origin including those from Norway and Iceland. However, it is worth noting that tag recaptures from Scottish fish (part of the southern European complex as defined by ICES) have been observed in East Greenland and were reported in this and other studies. Jensen and Lear (1980) carried out drift netting operations in the Irminger Sea and also reported tag recapture data from the East Greenland fishery. During research drift netting they captured 80 salmon, 77 of which were 1SW fish (destined to be MSW fish on return to home waters). Circa 79% of the salmon caught were estimated to be fish of European origin based on discriminant analysis of scales. Tag recaptures from the commercial fishery in East Greenland (1965-77) yielded 24 tags from fish tagged as smolts in home waters. Of these 24 tags, eight were of European origin, two coming from Scotland (Rivers North Esk and Tummel). Taken together the limited data for East Greenland and the Irminger sea indicate that these areas are probably less important for Atlantic salmon generally, and Scottish salmon in particular, than West Greenland. Jensen and Lear (1980) reported that historical attempts to fish the area by Danish vessels heading to Greenland were generally unsuccessful citing an occasion in 1972 when deployment of 900 drift nets yielded only six salmon.

The Faroese fishery has been relatively well documented. At various times, long-line fisheries operated at various distances from the coast, mostly to the north of the islands. Autumn fishing took place close to the islands, with winter fishing moving progressively north (Hansen and Jacobson, 2003). As it developed, the fishery tended to centre on northern Faroese territorial waters for winter and spring fishing and exploited mainly MSW fish. However, in earlier years (1969-79) exploratory fishing was carried out nearer to the Faroese coast.

Data are available on the numbers of fish which had previously been tagged as smolts caught in the fishery by country of origin. Data are also available from experiments in which sub-adult fish were tagged in Faroese waters and subsequently recaptured in home waters. Jakupsstovu (1988) investigated the proportion of fish that were tagged as smolts in home waters and subsequently caught at Faroe. He concluded that the proportion of fish of Scottish and Irish origin was relatively small compared with Swedish and Norwegian fish.

In apparent contradiction to the findings of the smolt tag returns, an adult tagging programme in Faroe between 1969 and 1976 (Jakupsstovu, 1986) indicated a high contribution of Scottish salmon to the Faroese fishery. Of the 90 fish tagged in Faroe and recaptured in home waters, 33 came from Scotland. Subsequent tagging work reported by Hansen and Jacobson (2003) again tagged adult fish off the Faroe Islands. However, on this occasion the proportion of Scottish tag returns was lower, at only 12 of 108 tags. After accounting for home water exploitation and tag reporting rates, Scottish fish were estimated to be the second most prevalent in the fishery, contributing ca. 20%, with the Norwegian contribution estimated at 40% (Hansen and Jacobson, 2003). Scottish salmon tended to be more prevalent in the autumn (November – December) rather than the winter fishery (February-March) and included fish from the Spey, Brora, Tay, North Esk and Dee.

There are clear differences in the findings of the two adult tagging studies. Hansen and Jacobson (2003) attributed the disparity to differences in the areas fished in the two studies. In the first study, fishing took place in close proximity to the Faroes and also to the south of the islands. This study tagged a large proportion of 1SW fish, at least some of which were heading west as there were subsequent recaptures in Greenland. In the later study the great majority of fish were caught to the north of the Faroes and comprised primarily 2SW fish. This view of temporally and spatially variable stock contributions to the Faroe fishery supports earlier work by Jacobsen *et al.,* (2001) where it was suggested that southern European fish contributed more to the early winter fishery and northern European fish contributed more to the later winter fishery.

The results of these studies have been summarised and reported in more detail elsewhere (ICES, 2007). In a Scottish context, however, it is known that adult or sub-adult salmon from Scottish rivers pass through or make use of areas around West Greenland, East Greenland and the Faroe Islands. The Scottish contribution to the West Greenland fishery was considered to be a substantial part of the total European contribution suggesting that many Scottish MSW fish used this area for feeding. Information for East Greenland, albeit scant, indicates that these waters contain MSW Scottish salmon at some times. In Faroese waters, the contribution of Scottish fish to the mixture of national stocks is again substantial and, in this case, they occur at both the 1SW and MSW sea-age stages depending on the area fished and the time of year.

The West Greenland fishery operated between August and November. The limited data from East Greenland and the Irminger Sea were obtained between June and October. The Faroese fishery operated between mid-October and the end of May. Considering those fish destined to mature at the MSW stage, it is therefore possible that all the fisheries sampled the same cohorts of Scottish fish as they migrated northward and westward from Scotland to West Greenland and returned eastward to Scotland. For MSW fish, there is some supporting evidence that at least some fish pass through Faroese waters on their way to or from West Greenland as fish tagged in Faroe have subsequently been recovered in Greenland and *vice versa* (Hansen and Jacobson, 2003). On this basis, but in the absence of an explicit demonstration, some post-smolt and 1SW sub-adults of Scottish origin caught at Faroe could have been heading to Greenland. At a later stage, MSW fish caught at Faroe may have been returning to Scotland from Greenland. This is of significance because fish returning from or via Faroese waters are likely to approach the Scottish coast from a predominantly north-westerly direction.

Given that both the Faroe fishery and West Greenland fishery exploited primarily MSW fish (on return to home waters), there is considerable uncertainty as to the migratory behaviour and feeding locations of the large numbers of fish destined to return to Scottish rivers at the 1SW (grilse) stage. It is possible that some of the fish caught inshore and to the south of Faroe, or that some of those caught in the central Norwegian Sea as post-smolts by Holm *et al.* (2000), were destined to become Scottish 1SW fish. Indeed, this knowledge gap emphasises one of the most important constraints on interpretation; the Greenland and Faroese fisheries constitute a set of only two sampling points for the much larger area of ocean in which salmon are potentially represented. The concept that salmon tend towards broader, less clearly defined marine habitat use, making use of large scale ocean currents has been advanced by Tucker *et al.* (1999), Spares *et al.* (2007) and Dadswell *et al.* (2010). It therefore remains possible that Scottish fish maturing at a sea-age of 1SW or MSW return towards the Scottish coast from a wide range of locations and across a broad range of headings. Current research work due to report under the EU funded SALSEA-Merge project may provide some additional information in this respect.

In summary, tagged Scottish Atlantic salmon have been observed at locations extending from Labrador in the west to Faroe in the east. As far as the authors are aware, no tagged Scottish Atlantic salmon have been observed on the Norwegian coast. However, large proportions of Scottish MSW salmon are estimated to be present in West Greenland and Faroe. Adopting a conservative stance for the purposes of this report, it is necessary to consider that fish of both the 1SW and MSW sea-age classes may return towards the Scottish coasts across a broad front. The available evidence indicates that the marine origins of the fish are likely to be highly biased towards a range of locations to the north and west of the British Isles.

2.4 Coastal Migratory Routes for Adult Salmon

The coastal migration of Scottish Atlantic salmon has been the focus of considerable interest for nearly a century. Early work by Calderwood between 1913 and 1920 and subsequently by Menzies (1937-38) and Shearer (1952-88) have provided insights based on the tagging of adult fish in Scottish coastal waters and their recapture in other coastal, estuary or river fisheries. Further insights come from examining the spatial distribution of tag returns from adult fish previously tagged as smolts as they left Scottish rivers. Assuming that these fish would then return to their river of origin, a range of potential migratory routes is revealed.

Shearer (1992) presented a summary of the work carried out between 1952 and 1983. There is little value in repeating Shearer's summary although the salient findings are discussed below. Instead, this review primarily focuses on the early adult tagging studies which were not reported in detail by Shearer (1992) and are not so generally available. These early studies often benefited from relatively high sample numbers. Moreover, the distribution and abundance of coastal fisheries from which to obtain tag returns was more uniform at the time of the studies than later on, aiding interpretation of the data. Although historical records of fishing effort do not generally extend back beyond the 1950s, Menzies (1937) reported the existence of 1436 salmon bag netting stations around the Scottish coast. Furthermore, Calderwood (1913), in trying to find a suitable location for tagging, commented that *"…as almost all of the available places suitable for bag net or fly net fishing are already occupied in Scotland it became a matter of some little difficulty to decide upon a situation which would at once solve the purposes of our research without inconveniencing those fishing regularly for commercial purposes*". Both of these reports provide anecdotal evidence of substantial fisheries in Scotland which are no longer present. The number of net fisheries in Scotland has declined rapidly over time to the extent that very few coastal net fisheries still operate (Fig. 17). The relatively sparse distribution of coastal nets in recent decades means that coastal recaptures can be substantially skewed by local effort and thus further care is required in interpreting these more recent data.

In this report, coastal movement studies are presented from areas around the British coastline relevant to Scottish salmon, moving progressively north and west from Northumberland on the north east coast of England to Ardnamurchan on the west of mainland Scotland. The coastal adult tagging studies are supplemented by information on the coastal recapture of fish tagged as smolts in the rivers Dee (Aberdeenshire), Tay and North Esk.

Figure 5 shows the spatial distribution of tag recaptures, by aggregated districts, from fish caught and marked in the Northumberland drift net fishery during 1977. Full details of the work are presented by Potter and Swain (1982). However, for the purposes of this review, the main feature of interest is the overall direction of travel and the distribution of recaptures. As with other tagging studies it should be noted that the distribution is likely to be affected by filtering of subsequent fisheries and as such capture near the location of tagging is more likely than at a distance. It should also be noted that once fish have been captured they are no longer able to continue their journey and as such capture location may not reflect the intended final destination. Nevertheless, the data suggest a strong northward migration from Northumberland as far north as Aberdeenshire, with decreasing recaptures in more northerly regions. The exception to this appears to be for the Forth area. However, this could reflect locally limited salmon abundance or fishing effort at the time. Very few fish were recaptured moving south from tagging locations towards English rivers and Potter and Swain concluded that 94% of the fish caught in the North East England drift net fishery were heading for Scottish rivers.

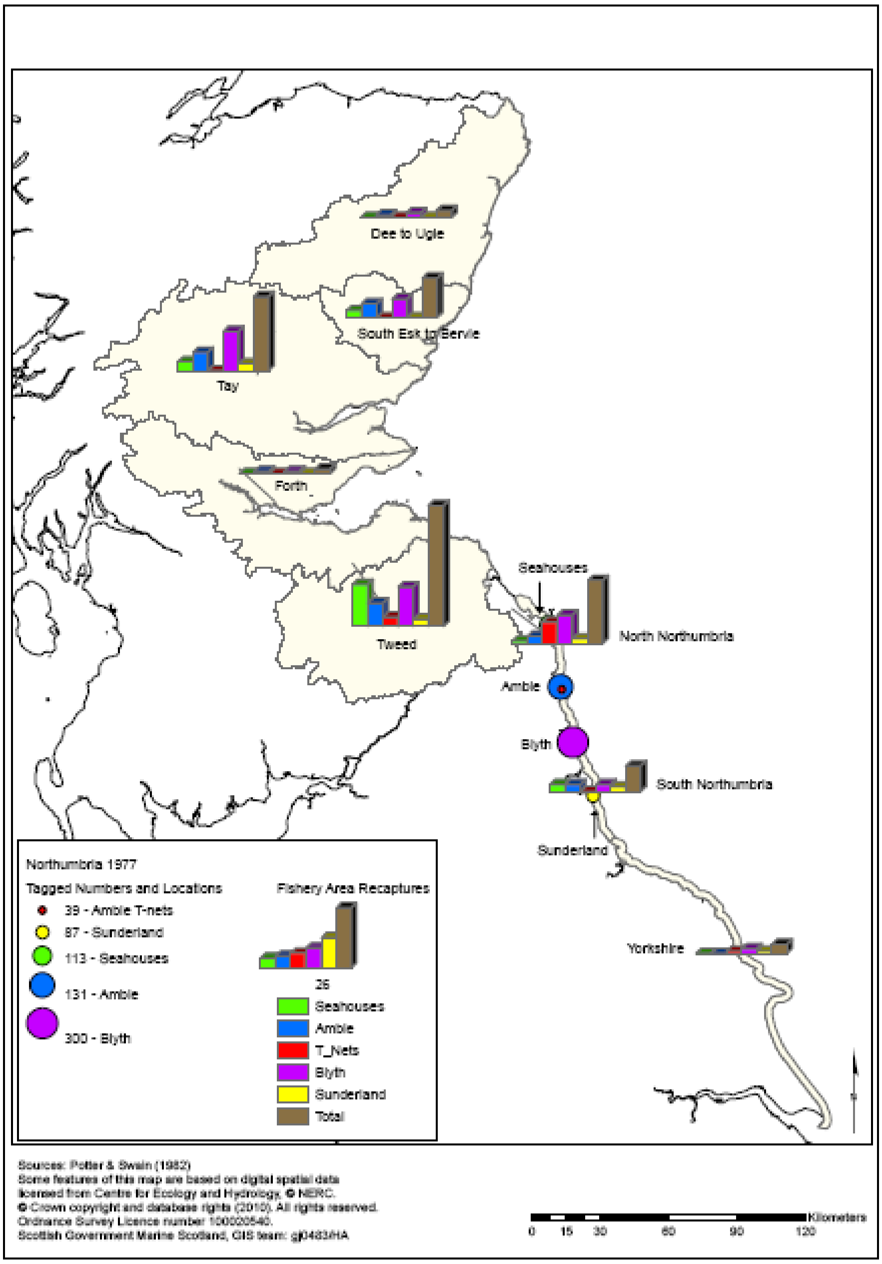

Figure 5. Coastal movement of salmon caught in the North east England drift net fishery (after Potter and Swain, 1982). Tagging locations are shown as coloured circles; the size of circles is proportional to the number of fish tagged. Bar charts indicate the number of fish recaptured, colour coded by tag location.

Moving progressively north, a series of tagging experiments was carried out in the Montrose area (Rockhall, 5 miles north and Bodin, 3.5 miles south of Montrose) between 1948 and 1955. The results of the experiments in 1948, 1950 and 1951 were reported by Pyefinch and Woodward (1955). They concluded that fish moved primarily in a northerly direction from the locations of capture and that the northerly extent of migration was the south shore of the Moray Firth. However, they also warned that the apparent extent of northerly migration may have been influenced by the small number of tagged fish. Consequently, the work was repeated in 1954 and 1955, using larger sample sizes (Shearer, 1958). The results of these studies are presented in Figure 6. The relative numbers of salmon and grilse were not separated in the studies, but overall 497 fish were tagged in 1954 and 201 tagged in 1955. In 1954 24.6% of recaptures came from north of the tagging site, 70.3% came from the Rivers North and South Esk and only 5.1% came from locations to the south. In 1955, 20.4% were recaptured to the north, 65.3% in the Rivers North and South Esk and 14.3% to the south (largely River Tay, but as far south as the Tweed). From the available information collected over five years of tagging it would appear that most of the fish caught in the area around Montrose are heading for the nearby Rivers North and South Esk. If these fish are excluded from consideration, then fish move both north and south, but overall the predominant direction of movement is towards the north as far as the south shore of the Moray Firth.

Calderwood (1914) carried out a series of tagging experiments on the Black Isle between 1913 and 1914. Fishing in 1913 was carried out between May and the end of August, capturing and tagging 210 salmon. Of these, 31 were recaptured, 16 to the north and 12 to the south or east. In 1914 fishing again commenced in May and continued through to late September. This time 154 salmon and 411 grilse were captured and marked and 38% were recaptured. Figure 7 shows the combined results of the 1913 and 1914 tagging programmes. It can be seen that fish moved north, east and south of the tagging locations and no overall pattern of movement can be determined, with fish moving as far north as the River Fleet and as far east and south as the Forth. The majority of recaptures however, were within 50 miles of the tagging site. Calderwood (1914) suggested that the limited geographical extent of the migrations was likely to be a genuine feature of the study rather than an artefact of sampling given the ubiquitous nature of coastal nets.

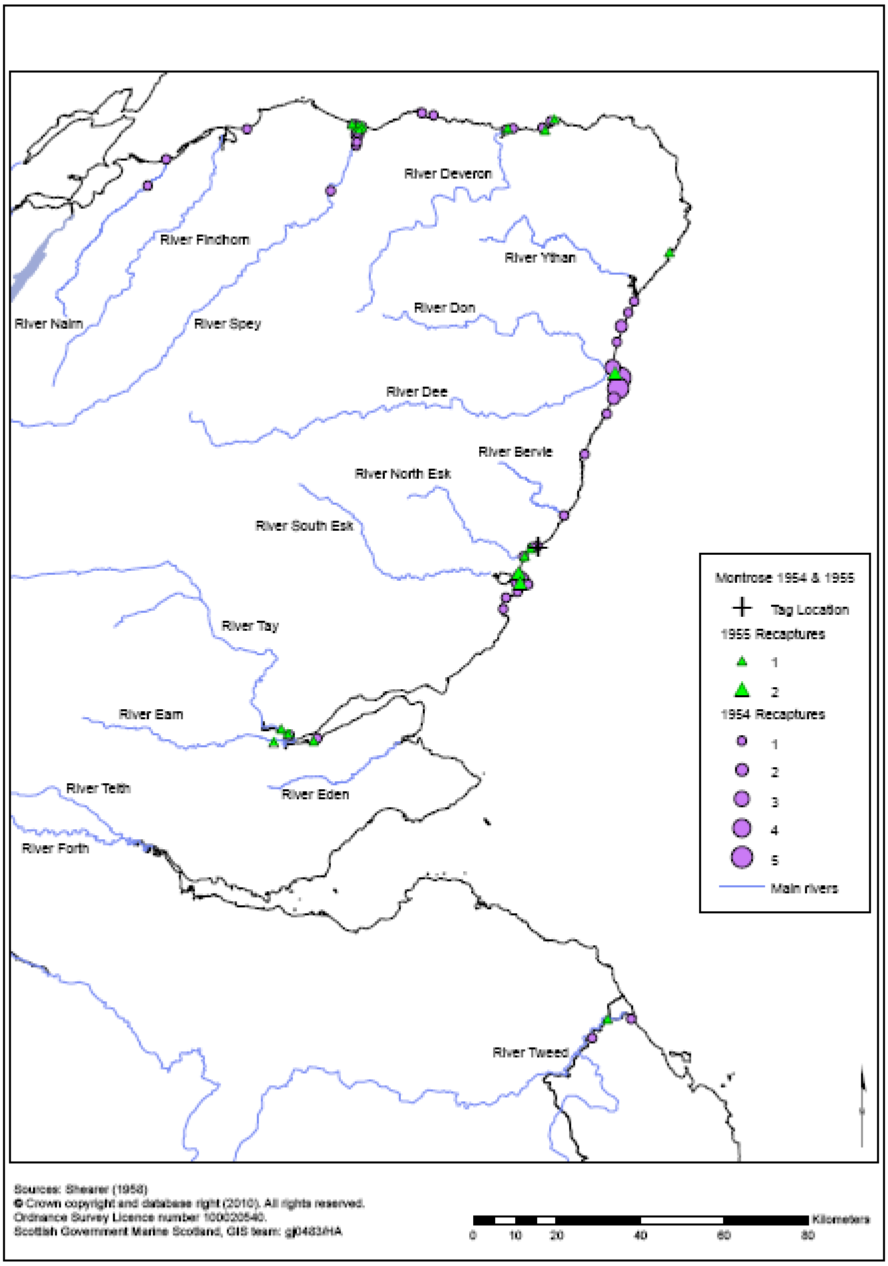

Figure 6 Map showing the distribution of coastal recaptures of fish tagged at Rockhall, 5 miles to the North of Montrose (after Shearer, 1958). Circle sizes are proportionate to the number of recaptures from a particular location.

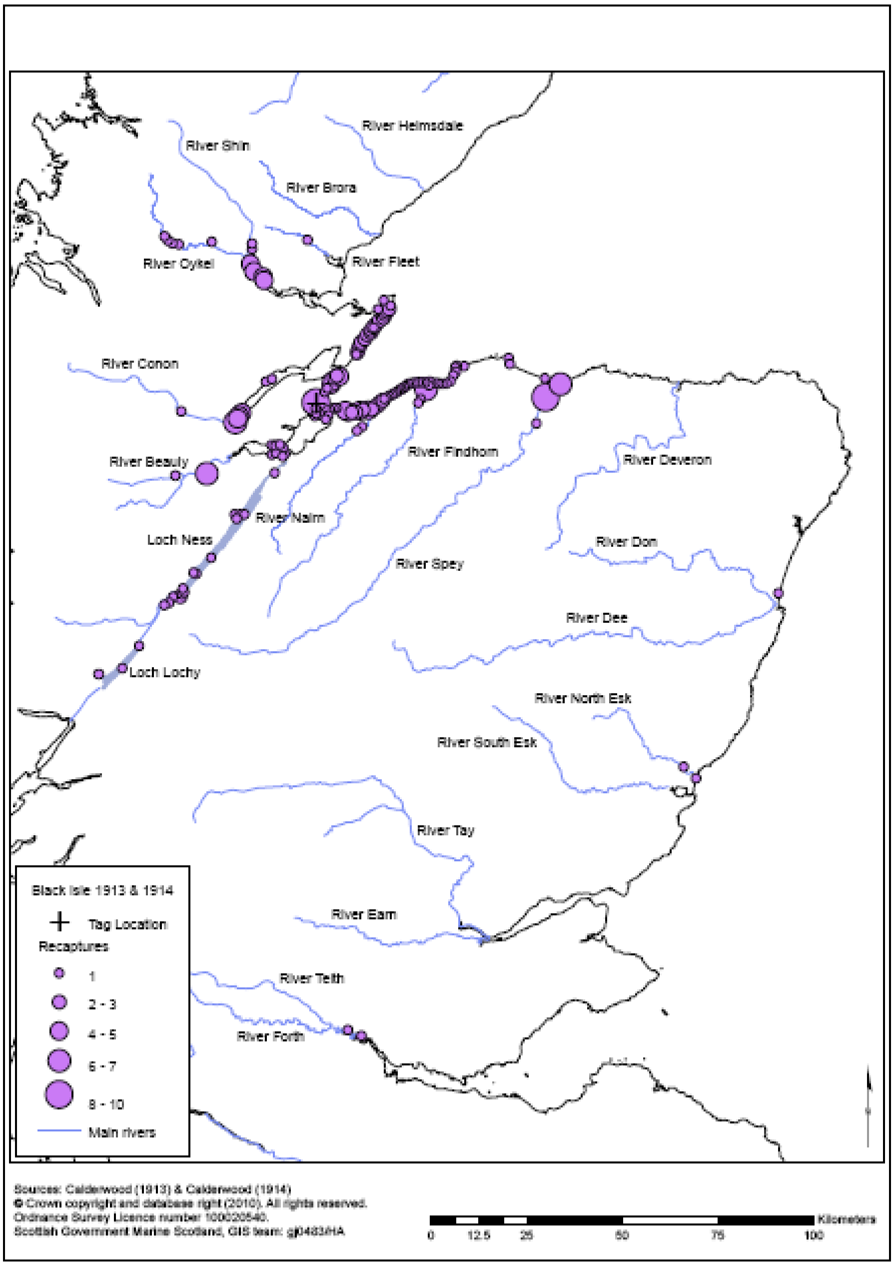

Figure 7 Map showing the distribution of coastal recaptures of fish tagged on the Black Isle 1913-14 (after Calderwood, 1914). Circle sizes are proportionate to the number of recaptures from a particular location

Following work on the Black Isle, Calderwood moved tagging north in 1915 to the coast of Sutherland between Brora and Helmsdale. Tagging took place between 22 April and 13 August, catching 378 salmon and 1295 grilse. Recaptures included 105 salmon and 322 grilse. The location of recaptures is shown in Figure 8. Salmon and grilse were not differentiated in the original maps and thus it has not been possible to do so in this report. From this work, Calderwood noted that almost twice as many fish headed north as south, but that a wide range of movements were observed. Particularly high densities of recaptures were obtained between Berriedale and Lybster, with extreme northerly movements observed through the Pentland Firth.

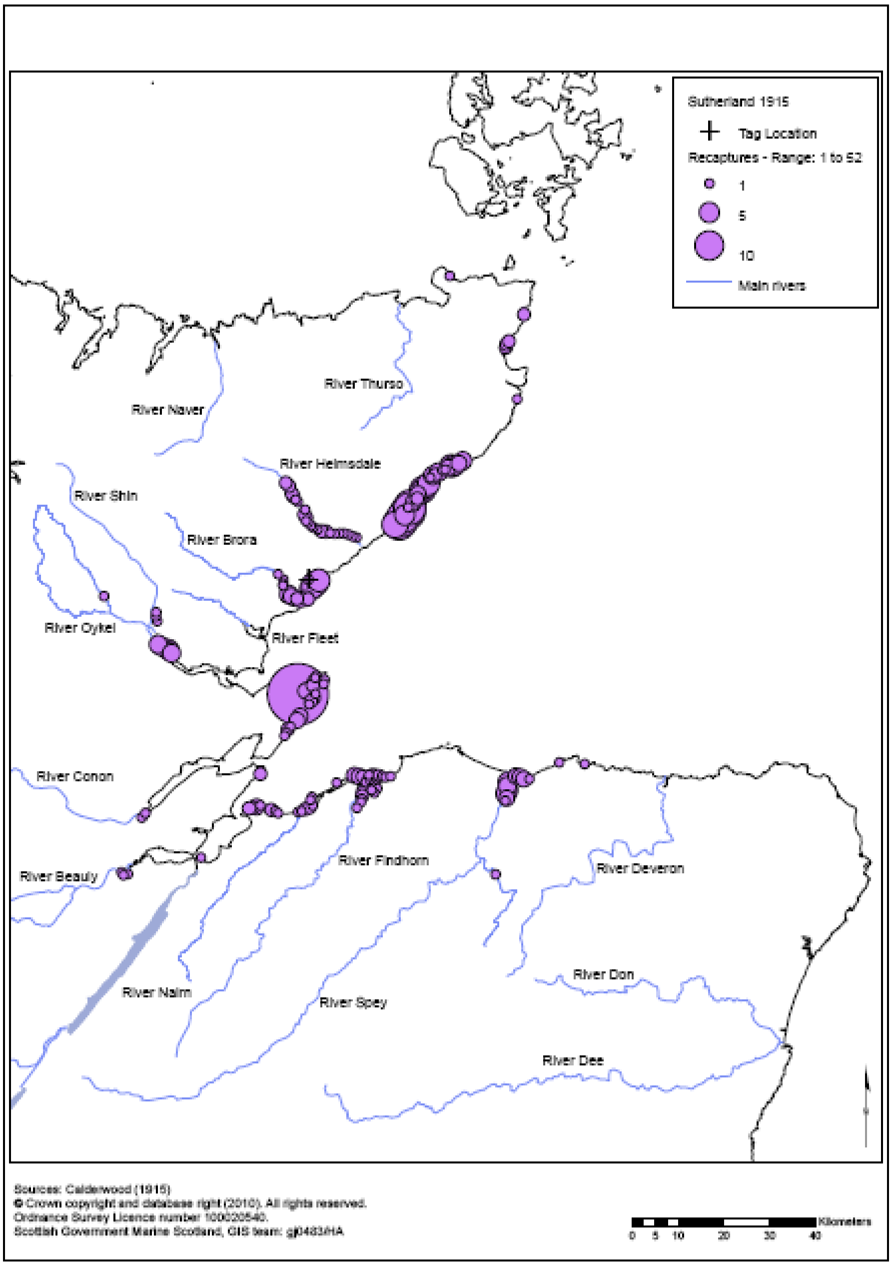

Figure 8 Map showing the distribution of coastal recaptures of fish tagged on the coast of Sutherland in 1915 (after Calderwood, 1915). Circles are proportionate to the number of recaptures from a particular location.

In 1920, tagging experiments were carried out in Thurso Bay, in the Pentland Firth on the north coast of Scotland. The location was chosen due to problems in deploying nets in the Pentland Firth area due to strong tidal flows and the generally low number of tag returns from the area as a consequence of the lack of nets. Given the location of the nets close to the River Thurso, it is of little surprise that many recaptures came from the river, rather than coastal nets (Fig. 9) and as such this study provides relatively little information on actual coastal movements. Tagging took place between 10 May and 15 September. In total 478 fish were marked, 142 of which were grilse, and 65 fish were recaptured. Most of these (38) were re-caught in Thurso Bay or in the river, 22 travelled west and five travelled to the east, being re-caught in Dunnet

Bay and beyond Duncansby Head in Sinclair Bay and the North-East coast near Wick.

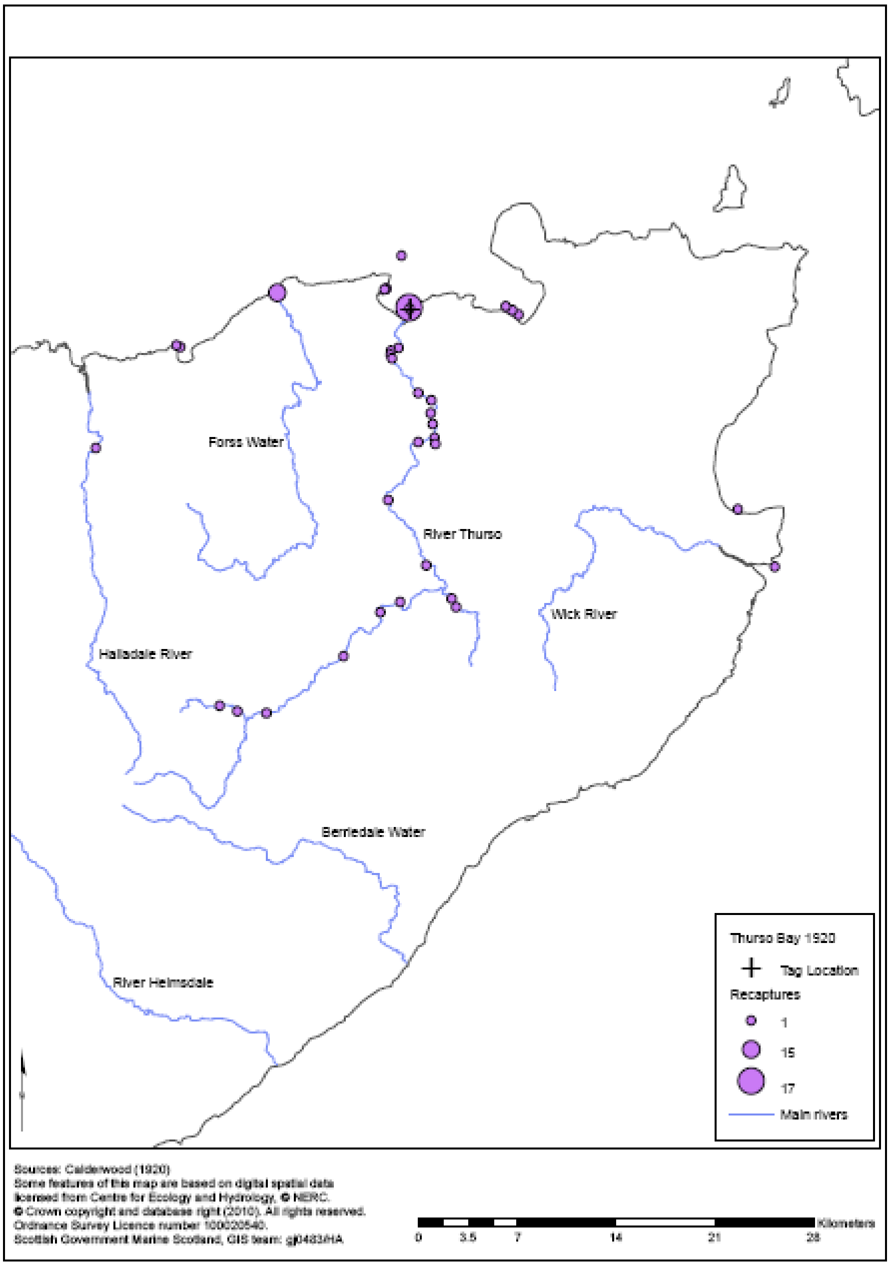

Figure 9 Map showing the distribution of recaptures of fish tagged in Thurso Bay (1920) (after Calderwood, 1920). Circle sizes are proportionate to the number of recaptures from a particular location.

In 1921 further work was carried out on the north coast at the Kyle of Tongue. Details of the work are not readily available, but Menzies (1937) reported that eight fish were re-caught at locations ranging from the Spey in the east to the Ewe in the west. This was the first time that fish had been recaptured on the west coast and led to follow up work in 1936 at Loch Inchard, 12 miles to the south of Cape Wrath (Fig. 10)

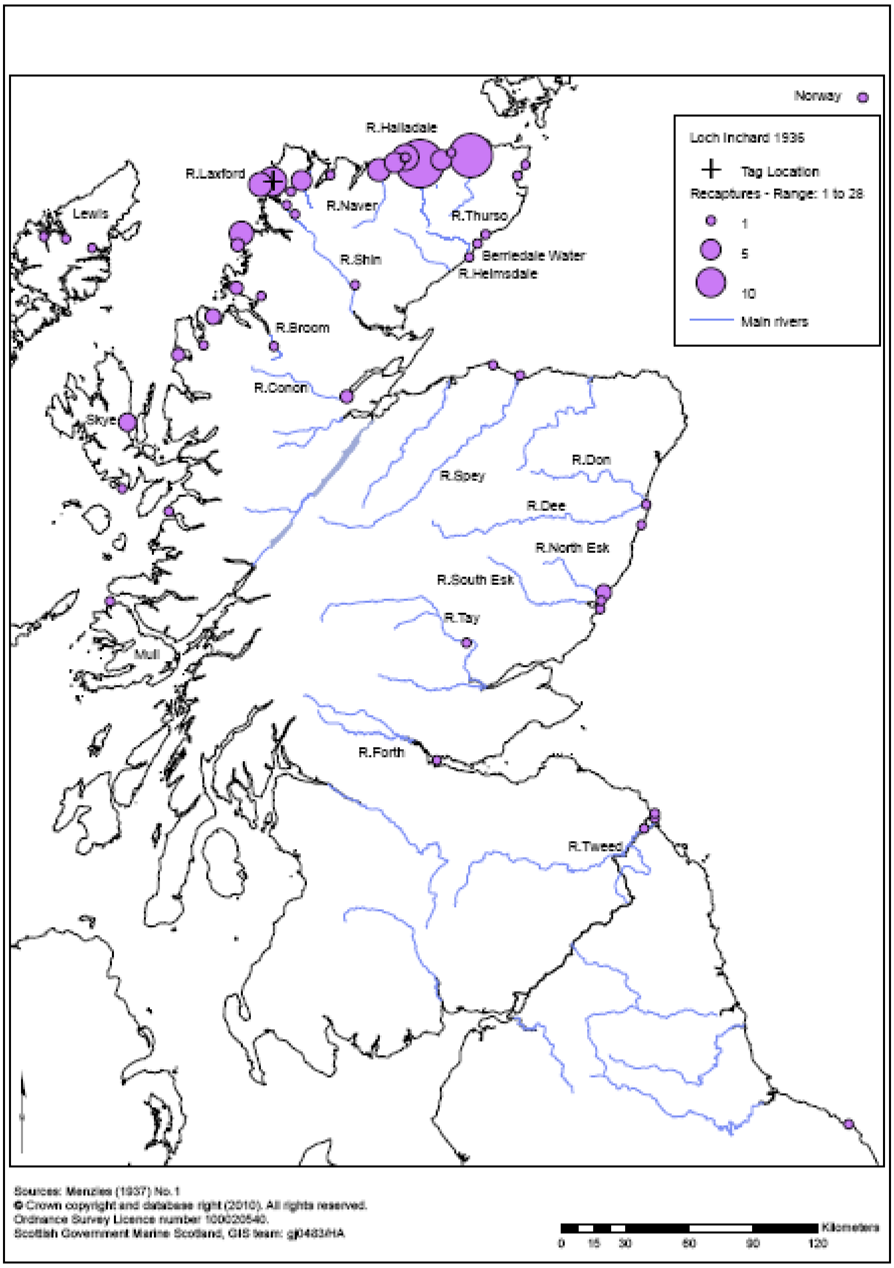

Figure 10 Map showing the distribution of recaptures of fish tagged at Loch Inchard (1936) (after Menzies, 1937). Circle sizes are proportionate to the number of recaptures from a particular location.

Netting at Loch Inchard took place between May and October, with 1255 fish (1006 grilse and 249 salmon) tagged. Of the fish tagged, 147 were recaptured, with grilse significantly more likely to be re-caught. The distribution of recaptures indicates that fish were more likely to be caught to the north and east (105) than to the south (40). Of the 20 salmon tagged and recaptured, six were taken on the north, six on the east and eight on the west. Of the 125 grilse recaptured, 93 went east and 32 went south. There was therefore a strong directionality to recaptures, which did not vary seasonally over the time fished. As expected, more fish were caught close to the point of tagging than at distance. However, fish were caught as far away as the Yorkshire coast and included recaptures in, or at the mouth of, many of the major east coast rivers including the Conon, Spey, Dee, Tay and Forth. Fish were also caught in coastal areas near Montrose and the Esk rivers.

Menzies (1937) suggested that the actual proportions and distribution of recaptures may not reflect the true distribution given spatial variability in the number of nets and effort employed, which was greater on the north and east coasts than the west. Therefore even in these earlier years where coastal netting was more ubiquitous, the distribution of fisheries could skew recapture data. Nevertheless, the data do indicate that fish captured on the northwest coast were often travelling towards the east and subsequently ended up in most of the major east coast rivers. It is also interesting to note that two fish were recaptured in Norway indicating that the Pentland Firth, or the area to the north, may be a migratory route for fish from other countries as well as the UK. From the scale data available and the direction of fish movement after tagging Menzies (1937) concluded that fish of many rivers were present in the north west of Scotland, probably utilising feeding grounds to the north or north-west. This hypothesis is consistent with modern understanding as summarised in Section 2.3 above.

In 1937, tagging was repeated on the north west coast of Scotland, this time 20 miles south at Raffin (Fig. 11). Fishing again took place between May and August. Salmon captures were greatest in May, with grilse captures greatest in July. The tagged fish included 324 grilse and 124 salmon, of which 58 were recaptured. The distribution of recaptures appeared to vary for salmon and grilse and therefore also to vary seasonally, such that a greater proportion of recaptures occurred on the north and east coasts early in the season (when salmon were more prevalent) and west coast later in the season. In total, seven salmon were recaptured on the west coast and 16 on the north and east coasts. Of the 33 grilse that were re-caught, 19 remained on the west and 14 were caught on the north and east. In general, the work at Raffin yielded similar results to that at Loch Inchard further up the coast.

In 1938 a pair of tagging experiments was carried out to the south of previous tagging studies on the west coast (Fig. 12). Fish were tagged from commercial fisheries at Soay (off the south west coast of Skye) and Fascadale (west coast mainland). At Soay 100 fish, primarily MSW salmon, were tagged between April and May. Tagging at Fascadale took place between the end of May and July, marking 280 fish, primarily grilse. Of the 22 salmon recaptured from the marking at Soay, 18 were caught on the north and east coasts, extending as far south down the east coast as the Tay (Fig.10). The pattern of recaptures from Fascadale differed markedly from that at Soay, with most fish (29 of 35) being caught within a 30-40 mile radius. Of the remaining fish, three were re-caught in Ireland, one in North Wales, two in the Cromarty Firth, one north of Montrose and one in the Tay.

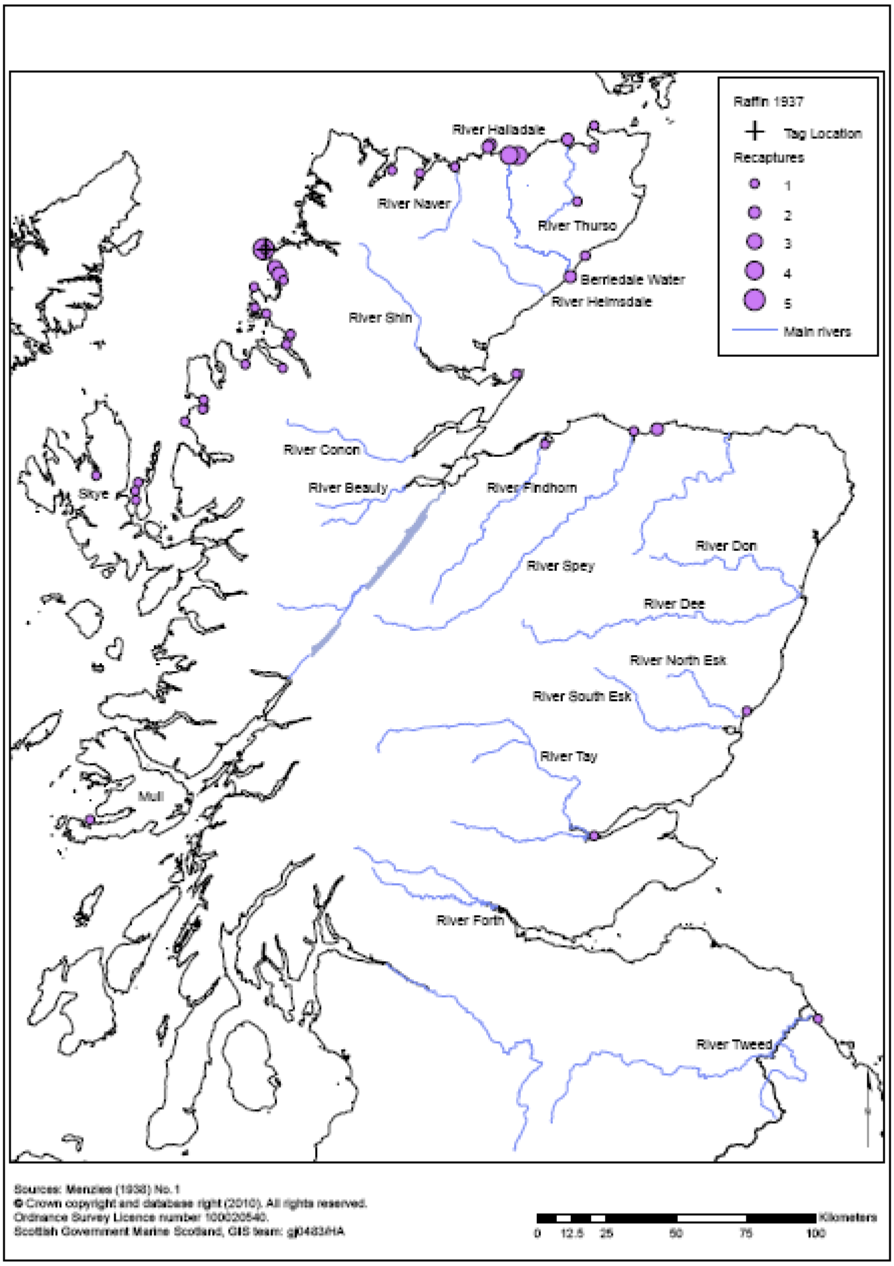

Figure 11 Map showing the distribution of recaptures of fish tagged at Raffin (1937) (after Menzies, 1938a). Circle sizes are proportionate to the number of recaptures from a particular location.

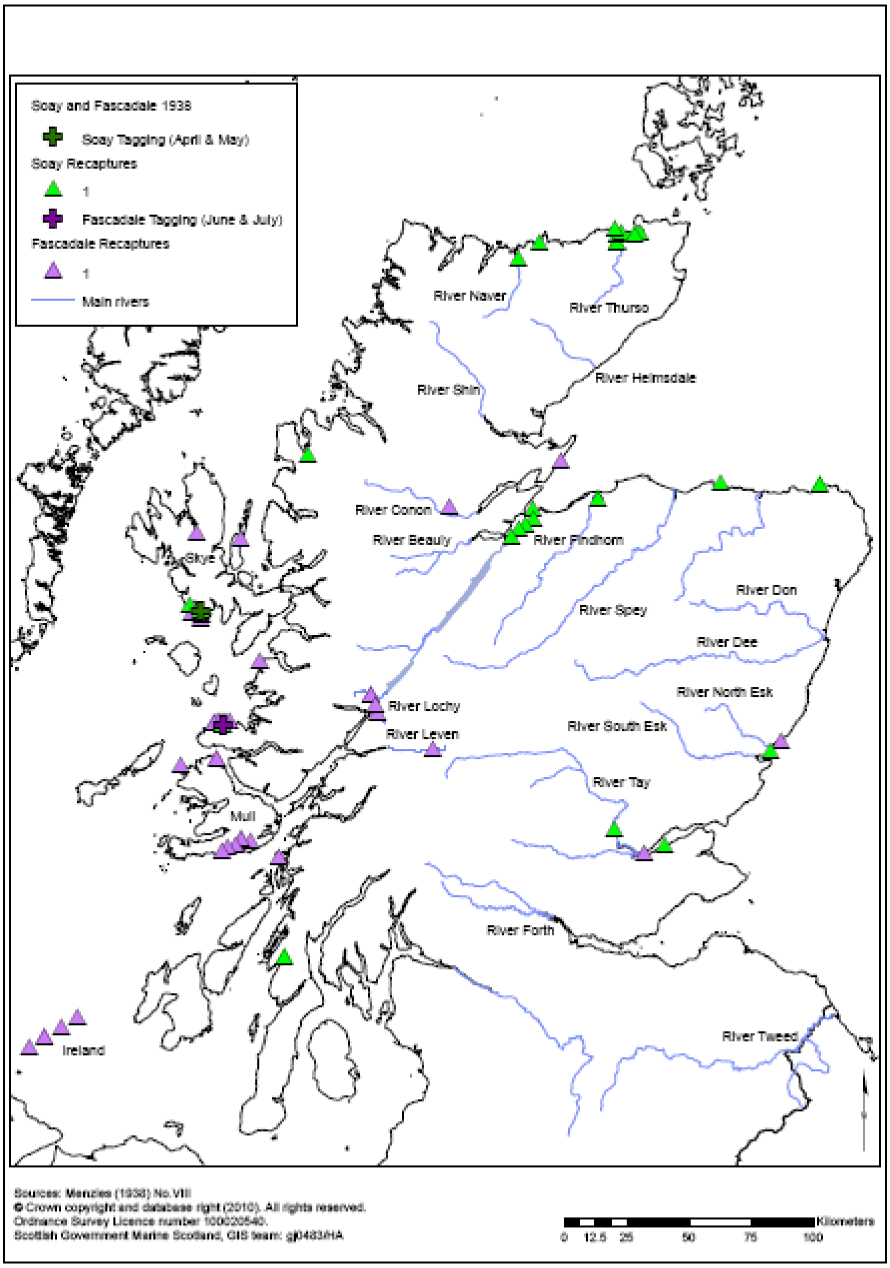

Figure 12 Map showing the distribution of recaptures of fish tagged at Soay and Fascadale (1938) (after Menzies, 1938b). Circle sizes are proportionate to the number of recaptures from a particular location.

Shearer (1992) reported a series of tagging studies conducted between 1952 and 1988. The experiments from the Montrose location that were covered in his summary are also covered in this report. The remaining studies generally showed similar patterns of movement to those reported earlier by Calderwood and subsequently Menzies for nearby tagging locations in the same areas. One feature of particular interest in the work reported by Shearer (1992) was the number of fish tagged at Berriedale on the north east coast which were subsequently caught on the north coast. Previous tagging work carried out by Calderwood between Brora and Helmsdale had indicated that fish passed from the east through the Pentland Firth to the north coast. However, the work reported by Shearer indicates that this may be relatively common.

In addition to the coastal tagging studies identified above, it is also possible to obtain some indication of potential migratory routes from returns of fish tagged as smolts in their native rivers. Figures 13 and 14 show the recapture locations of fish tagged with externally visible Carlin tags as smolts leaving the Girnock Burn on the Aberdeenshire Dee. For the purposes of this report, fish caught by rod and line on the Dee have been excluded. For 1SW fish (Fig. 13) it can be seen that the majority of recaptures were in close proximity to the Dee, although substantial numbers were also caught in the proximity of the Esks and the Tay. However, single fish were also captured around the west, the north and the Moray Firth coasts. It should be noted, as with previous examples, that the distribution of recaptures is likely to have been affected by the magnitude and seasonal distribution of local fishing effort. Given the relatively recent nature of these data, this is likely to have been a considerably more substantial problem than for historical data as netting effort has been more sparse and patchy in recent years (Fig. 17). Nevertheless the plots provide some indication of the geographical range and relative magnitude of recaptures. Figure 14 shows the same pattern for MSW fish. In this case it can be seen that the majority of recaptures were in the area around the Esks and Dee, although single fish were also caught in the Tay and to the south of the Tweed on the Northumberland coast and around the Moray Firth. There were no recaptures on the north and west coast of Scotland, although two fish were caught in Ireland.

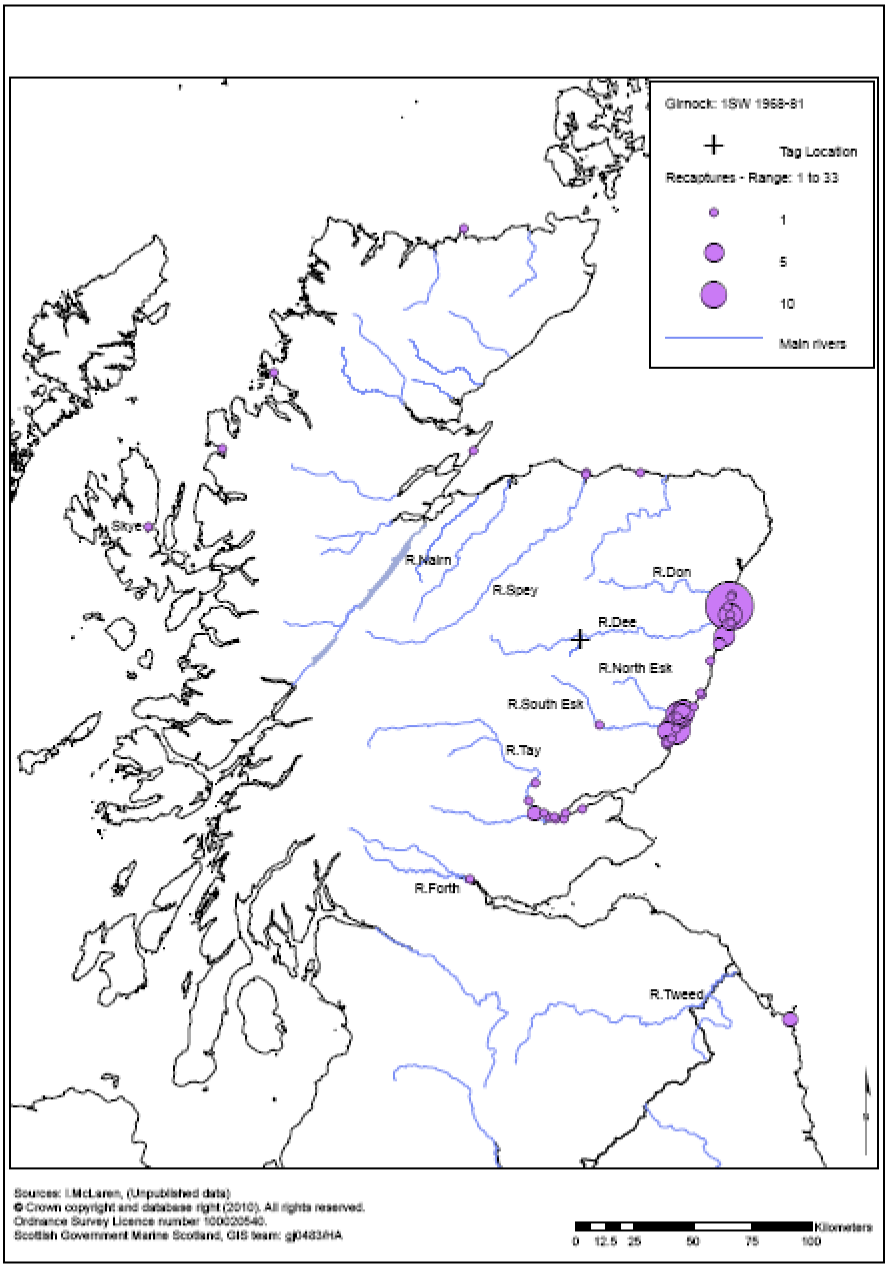

Figure 13 Map showing the distribution of recaptures of 1SW (grilse) tagged in the Girnock Burn as smolts (1968-81). Circle sizes are proportionate to the number of recaptures from a particular location.

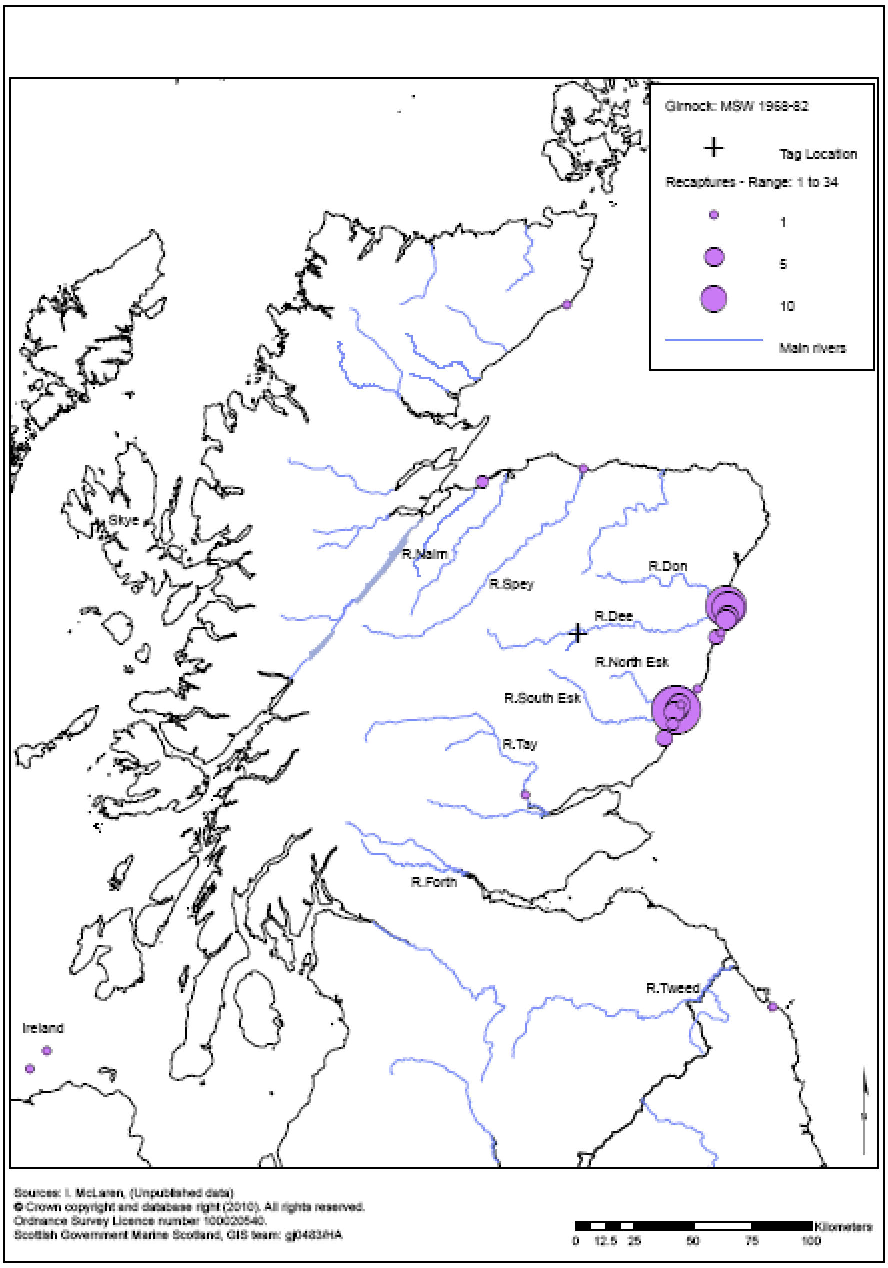

Figure 14 Map showing the distribution of recaptures of MSW (salmon) tagged in the Girnock Burn as smolts (1968-81). Circle sizes are proportionate to the number of recaptures from a particular location.

Figure 15 shows similar data for the river Tay system. Data are provided only for smolts tagged with external tags. Data are aggregated for the tributaries Almond (1968 to 1974) and Tummel (1967 to 1973; 1975 to 1988) and for salmon and grilse. The data include all methods of coastal capture, excluding net and coble, which dominated tag returns in the Tay system. Tagged fish were recaptured off the west, south and north coasts of Ireland, around the west and north coasts of Scotland and in relatively large numbers off the south east coast of Scotland and the north east coast of England.

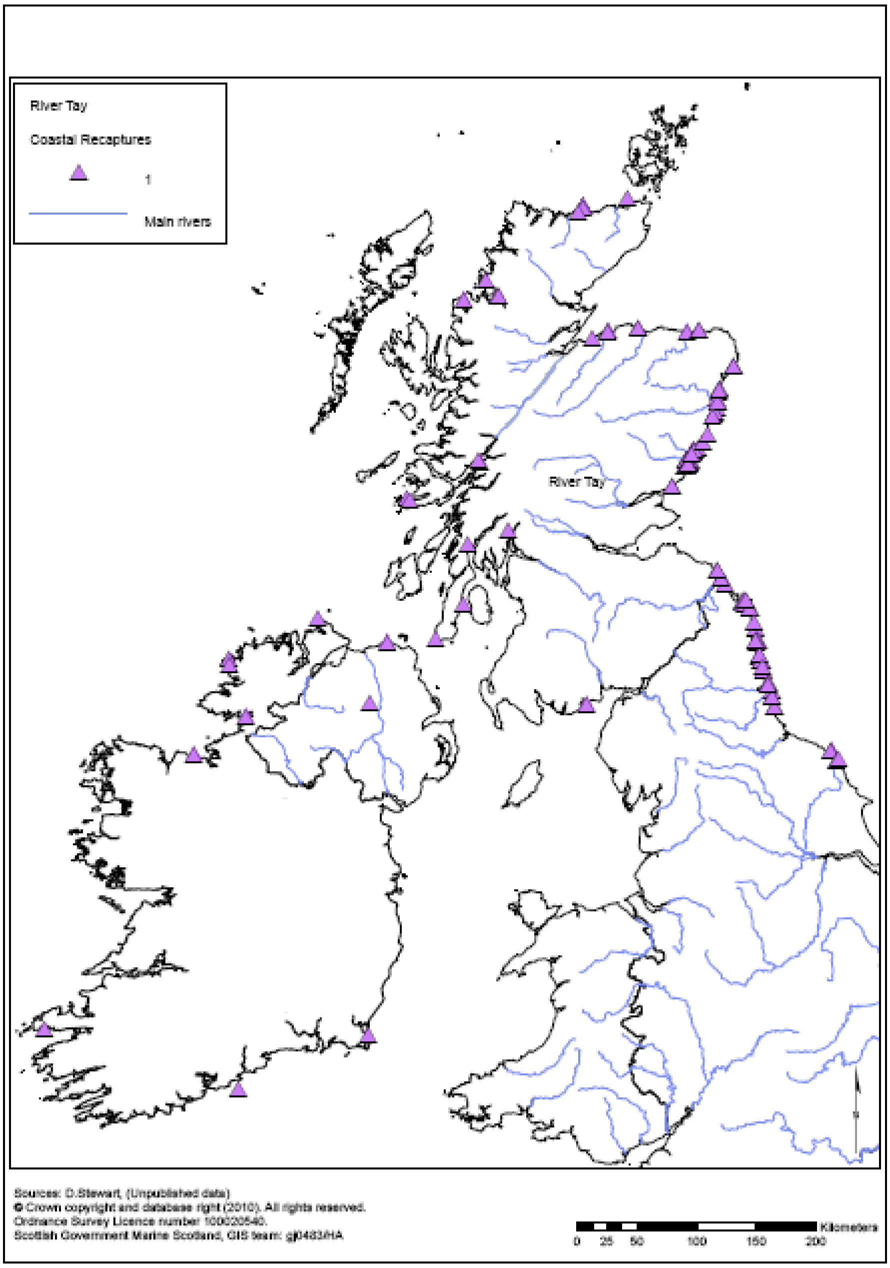

Figure 15 Map showing the distribution of recaptures of salmon (including grilse) tagged in the River Tay (Almond and Tummel) as smolts (1967-88). Triangles represent individual tag recaptures.

Unfortunately, similarly detailed maps of the distribution of salmon recapture locations are not currently available for the North Esk, the other Scottish river for which substantial smolt tagging data is available. However, data aggregated by river district were prepared for a recent review of mixed stock fisheries (Crawley, 2010). These data covered the period 1991-2007 for externally tagged fish. The ranking of recaptures among districts was generally consistent between methods (fixed engine, net and coble, rod and line), at least among the top three districts, which accounted for the majority of returns. When all methods of capture were grouped together, the majority of recaptures were within the North Esk and Bervie district (70% or 355 fish) followed by South Esk (17% or 84 fish) and Dee (7% or 33 fish) (Fig. 16).

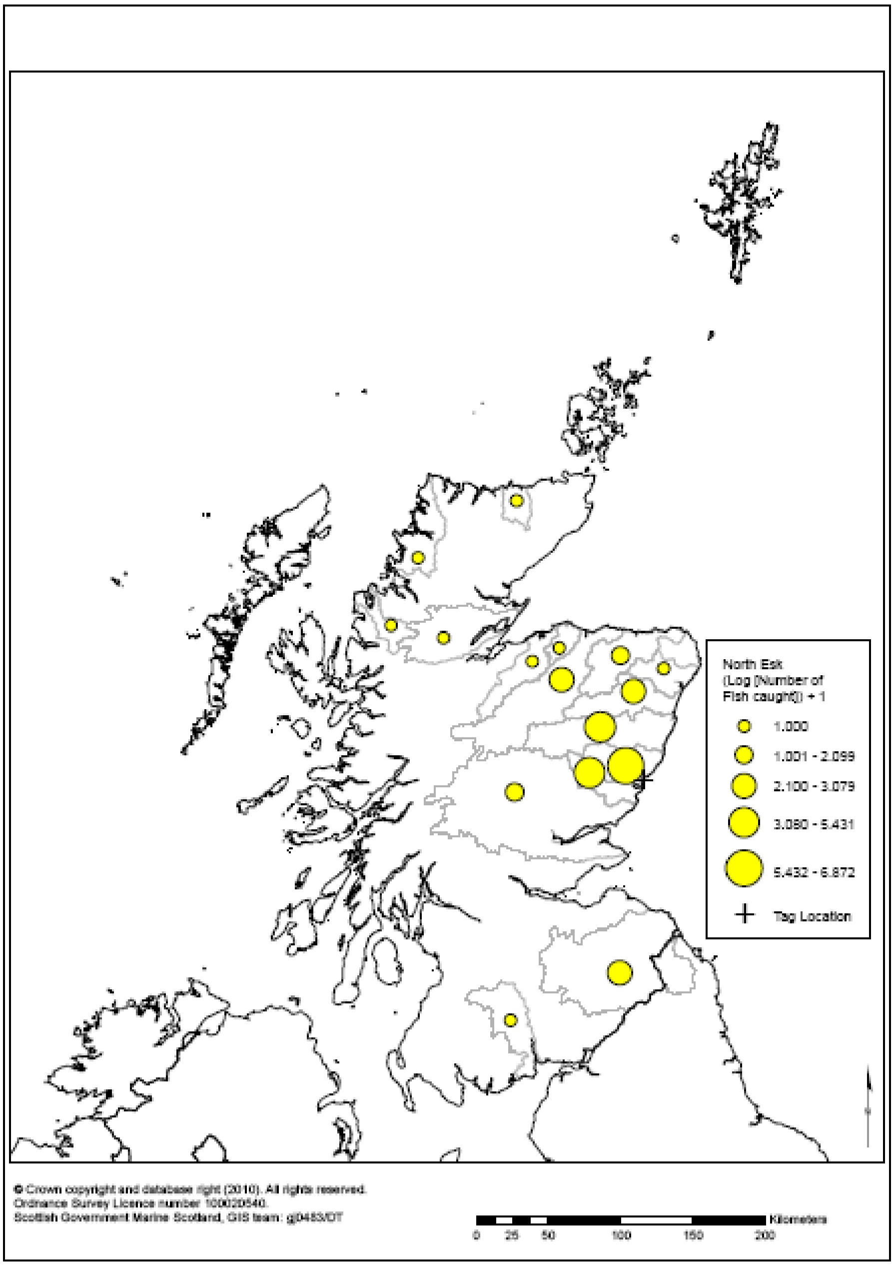

Figure 16 Map showing the distribution of salmon marked as smolts in the North Esk and subsequently recaptured.

Low numbers of fish were also caught in the Don (4), the Tweed (7), the Spey (5), the Deveron (3) and the Tay (2) districts. Single fish were observed in the Ythan, Lossie, Findhorn, Conon and Alness, Halladale and Strathy, Inchard to Kirkaig, Ewe and Nith districts. As with the data presented previously, the distribution of recaptures could be affected by the distribution of fishing effort, and this will be especially true for the North Esk, as much of these data were collected relatively recently when the distribution of coastal fisheries has been much reduced (Fig. 17).

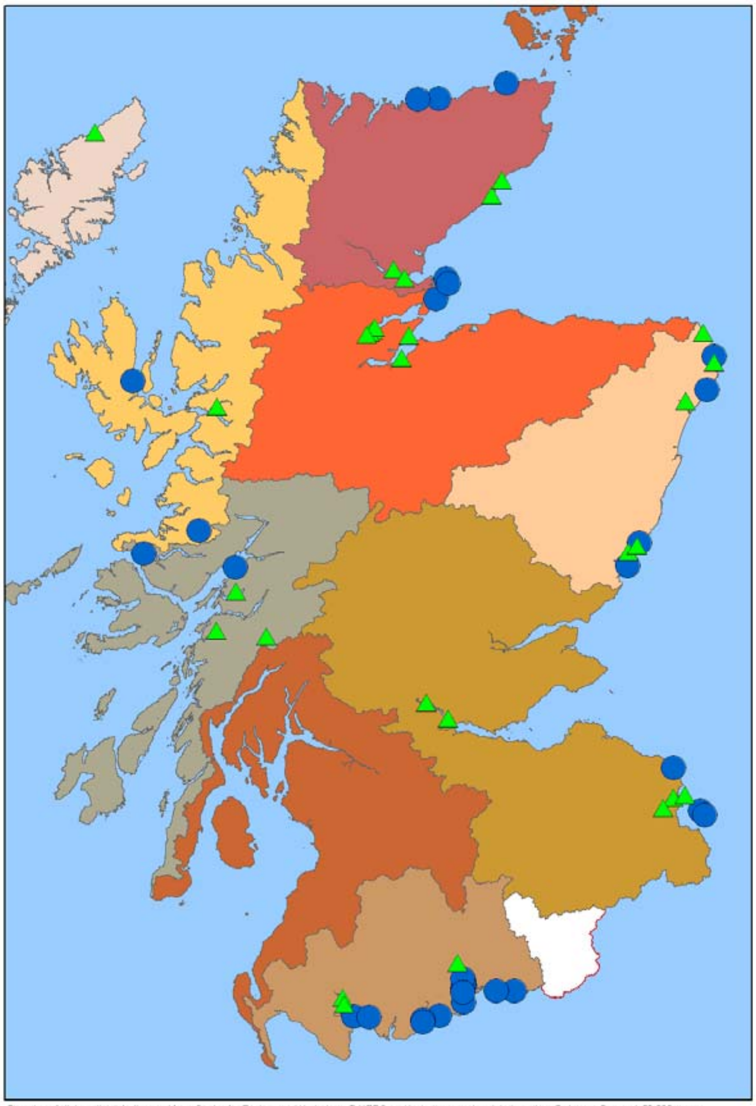

Figure 17 Map showing the distribution of net fisheries in Scotland in 2008. Fixed engine fisheries are shown as blue circles, net and coble fisheries are shown as green triangles.

Considering the work of Calderwood (1913, 1914, 1915 and 1920), Menzies (1937, 1938a, 1938b), Pyefinch and Woodward (1955) Potter and Swain (1982) and Shearer (1958, 1992), together with the available data for the Dee (Girnock Burn), Tay (Tummel and Almond) and North Esk, it is possible to begin to summarise the patterns of movement observed around the Scottish coast.

- On the south east coast of Scotland and north east coast of England, the general direction of salmon movement is northerly and this persists as far as the north Aberdeenshire coast.
- On the Black Isle and Sutherland fish appear to move in both a northerly and southerly direction.

- On the north and extreme north west coasts, fish appear to move both to the east and west, although movement to the east is more common.
- On the west coast, the patterns of migration for grilse (1SW) and salmon (MSW) differ. Salmon primarily head north and east, while grilse head both north and south.

This final observation reveals one of the potential problems with the tagging data reported here in that a high proportion of the observations available to this review were for grilse, which were more prevalent in the coastal nets during the summer months. Different sea-age groups were rarely differentiated in earlier or indeed later studies when the location of recaptures was mapped. It is likely that MSW salmon and grilse show different patterns of migratory movement for a number of reasons. For example, MSW salmon and grilse may use different marine feeding areas and consequently return to the coast from different directions. In addition, MSW salmon are also found predominantly in the north and east coast rivers, rather than the smaller west coast rivers which are more commonly dominated by grilse. Therefore it should be no surprise that MSW salmon returning to the north and west coasts are heading in an easterly and northerly direction, respectively.

Shearer (1992) proposed a simplified model of adult salmon migration which suggested that salmon return to the north and west of Scotland and then migrate around Scotland and down the east coast as far as Aberdeenshire. From Aberdeenshire southwards it was suggested that fish travel in a northerly direction having migrated south past their home rivers through the North Sea and approach the coast around Northumberland. At first inspection this conceptual understanding may seem reasonable especially for MSW salmon, where return to the coast was assumed from the north-west. However, data from the Moray Firth, Caithness coast, north and west coasts of Scotland suggest a considerably more complex pattern of movement with fish moving in both directions. In addition, as identified previously, it appears that both MSW salmon and grilse may return from either the north or west. If this is the case then an alternative conceptual model can be proposed whereby salmon and grilse return both to the north and west coasts of Scotland, and may even reach the north east coast directly having passed Orkney and Shetland. After they reach the coast they move towards their home rivers, giving apparently variable patterns of migration for a given tagging position. Given that MSW salmon rivers dominate the north and east coasts, the dominant direction of movement for MSW fish caught on the west will be north and east. However, for grilse, the pattern of movement would depend on where they reach the shoreline and where their native river was located. For the east coast rivers south of Aberdeenshire the pattern appears clearer, with fish generally moving in a northward direction from the Northumberland coast, in agreement with Shearer (1992).

One of the major constraints on the above interpretation is the lack of information on adult salmon in the waters around Orkney and Shetland. Despite the large number of successful fisheries that have been pursued on the northern coasts of Sutherland and Caithness at various times, it is perhaps surprising that no matching fisheries are reported from either the Orkney (including the northern shores of the Pentland Firth) or the Shetland Islands. Orkney and Shetland lack salmon rivers but Orkney in particular lies on or near a line of direct passage to the Scottish mainland from Faroese waters. If this negative evidence can be taken to reflect the low abundance of fish on the Orkney and Shetland coasts, including the inter-island sounds, it would suggest that migratory routes in northern Scottish waters may be biased towards the mainland coast. At present however, there remains insufficient information to determine the relative importance of these areas.

2.5 Adult Salmon - Migratory Behaviour

While tagging studies provide some indication of the directions moved by fish and the spatial distribution of fish from particular rivers they do not provide important detail on how fish move in coastal waters in terms of distance offshore or swimming depths. These additional data can be obtained through manual tracking of individual fish to provide information on direction, speed of movement and location relative to shore, and through tagging and recovery of fish with data storage tags to provide information on swimming depths and temperatures.

There are relatively few detailed studies of adult salmon movement in Scottish coastal waters, or more generally. Hawkins *et al.* (1979) tagged six grilse off the coast of Scotland at Rockhall near Montrose in 1978. They established that fish moved with the tidal currents including on and offshore movements. However, their mean speed often exceeded that of the tide suggesting that movements were not entirely passive. The behaviour of three of the grilse tracked close to the shore suggested that once fish were close to the river, they changed their behaviour from swimming with the current to swimming against it. The three remaining fish were tracked further offshore, although actual distances offshore were not reported. Subsequent work by Smith *et al.* (1980, 1981) suggested that when tidal movements were subtracted from fish movements, the tagged fish showed consistent directional movements which varied between fish. It was further hypothesised that the relatively slow swimming speeds were optimised for energy efficiency during migration. Importantly Smith *et al.* (1981) noted that six fish tagged from coastal nets in 1979 (2 salmon, 4 grilse) rarely approached the shore and travelled at distances of up to 17km offshore in contrast to the fish in earlier studies of which half were heading for the nearby North Esk, remaining inshore for much of the time.

Data on adult swimming depths are similarly sparse. However, Jakupsstovu (1986) tagged two salmon in 1985 and 1986 with acoustic tags in the ocean off the coast of Faroe. Depth sensitive tags revealed the vertical movements of the fish. Immediately after tagging the fish dived rapidly to depths of more than 100m. This was hypothesised to be a stress response to tagging. After this, fish returned towards the surface where there was a high degree of variability in the behaviour, with fish spending variable periods of time at variable depths ranging from near surface to 40 m. Periods near the surface were frequently punctuated by dives up to depths of ca. 160m. This early study indicated the range of depths potentially used by Atlantic salmon and hypothesised that the dives were associated with feeding. In the context of this review it is worth noting that work by Fraser (1987) indicated that grilse continued to feed in western Scottish coastal waters until early July based on an analysis of stomach contents.

Holm *et al.* (2005) captured and tagged 406 fish with data storage tags (DSTs) in the Norwegian Sea between 2002 and 2004. Only five tagged fish were recaptured from which to recover data. The recaptured fish all showed limited activity for 10-14 days following tagging, after which there was substantial variation in behaviour. Generally fish resided within 5-10m of the surface, although dives were also observed ranging from ca. 85-280m. The number and depth of dives varied widely between fish. It was suggested that fish were travelling to the coast and feeding at the same time.

Starlaugsson (1995) tagged 60 salmon returning to the coast of Iceland and relocated them 25-95km offshore, eventually recapturing them in the fjord where they were first captured. Most of the salmon spent most of their time within 4m of the surface. However, frequent diving was also observed in these fish to depths ranging from 10 to 123m, suggesting that diving behaviour is not exclusively an offshore phenomenon.

Overall, it appears that salmon typically spend most of their time close to the surface, but that they often dive, sometimes to great depth (up to 280m). It also appears that this behaviour persists late into the migration on the return to home waters.

2.6 Salmon Kelts

Kelts are fish which have spawned in the preceding autumn or winter, recovering in fresh water and the sea. In some cases, kelts can recover condition and return to spawn again, either in the following spawning season or following a full year of recovery in the sea (Menzies, 1911; Niemela *et al.,* 2006); these fish are known as repeat spawners (as distinct from maiden fish) and their status can be detected by scale reading.

In the context of this review it is necessary to establish the relative importance of repeat spawners to Scottish salmon stocks to inform the emphasis that should be placed on establishing the outward coastal movements of kelts versus the inward movements of returning adults. In general, the proportion of previous spawners returning to spawn in Scottish rivers is considered to be low. For example, data from the net and coble fishery (1981–2009) on the North Esk indicate that repeat spawners contribute, on average, only 0.84% of the total annual catch of salmon (range 0.04-1.54%, n=77,530, Julian Maclean pers. comm.). Data for other major east coast rivers indicates a similar proportion of repeat spawners ranging from 0.71% on the Tweed to 1.48% on the Dee (Table 1, Phil Bacon pers. comm.). However, it should be recognised that these figures apply only to the seasonal period over which the fishery operates and as such are unlikely to reflect the absolute proportion of repeat spawners returning to rivers as this may vary across the year.

	Dee	**North Esk**	**Spey**	**Tay**	**Tweed**
Years of Data	8	44	16	28	35
Min %	0.28	0.19	0.00	0.00	0.00
Mean %	1.48	0.84	0.83	0.86	0.71
St.Dev %	1.30	0.45	0.64	0.66	0.64
Max %	4.08	2.11	2.36	2.80	3.20
Sample size (n)	5949	77530	17773	25511	33430

Table 1 Summary statistics showing the percentage and variability of repeat spawners in the net and coble fishery of the rivers Dee, North Esk, Spey, Tay and Tweed together with the number of sampling years and the sample sizes (Phil Bacon, pers. comm.).

Data for other times, and for other Scottish rivers, suggest that the proportion of repeat spawners can be greater than the values cited above. For example, Menzies (1911) reported that previous spawners comprised 29% of a sample of returning MSW spawners from the Awe (n=45), with intermediate values of 5.6% and 8% reported for the Spey (n=106) and Forth (n=97), respectively. However, it should be noted that the sample sizes in these studies were rather low and the conclusions to be drawn must therefore be correspondingly tentative. Indeed, Calderwood (Menzies, 1911) added a subsequent note on the Awe fish, where he identified that of 22 fish examined subsequently, only one had spawned for a second time.

Outside of the UK, the proportion of repeat spawners also varies substantially between sites and years. Niemela (2006) reported that the mean proportion of repeat spawners (1975 and 2004) in the River Teno on the northern border between Finland and Norway averaged 5% (range 1-21%) of the total salmon catch (n=69,870). When gender was considered, on average 7% (range 1-29%) of females and 4% (range <1-14%) of males were repeat spawners. Jonsson and Jonsson (2004) summarised the findings of a range of studies across a broad geographic range. They reported that the percentage of repeat spawners in 17 Norwegian rivers ranged between 2% and 25%, with values of 7.3% for the Shannon in Ireland and 14% for the Maguadavic in Canada. Jonsson *et al.,* (1991) reported that the chance of repeat spawning decreased with fish size and sea age of maturity and that 1SW fish tended to spawn again the following autumn, while MSW repeat spawners returned the following year (biennial spawners). Given the available information it appears that the proportion of repeat spawners varies considerably between sites and years. For the single site for which there is good information in Scotland (the North Esk), it appears that repeat spawners are much less abundant than maiden fish. However, there is currently no basis to extend these findings to fish which approach the North Esk after the fishing season has ended or to fish in other Scottish rivers. On a precautionary basis, therefore, it is probably necessary to also consider the importance of kelt migrations from rivers to the ocean, on the same basis as the seaward migration of smolts and the return migration of maiden fish.

Unfortunately, there is very little information available on the migration or behaviour of kelts in a Scottish context. Early tagging studies e.g. Calderwood (1910) tended to capture, mark and recapture fish in the same river and consequently provided little or no data on coastal movements. More recently, limited behavioural work has been carried out in Norway to assess rate of movement and behaviour of kelts passing through Norwegian fjords. Based on tagging data, Halttunen *et al*. (2009) suggested that, as for smolts, migration through fjords is rapid and generally at shallow depths (mean individual depths of 0-15m).

In summary, data on the importance of repeat spawners to Scottish adult salmon returns are spatially restricted and often of limited sample size. Those data that are available suggest that the current contribution of repeat spawners is likely to be small. However, these data are temporally limited by the sampling period (the netting season) and may not be transferable between different geographic areas. Data from other countries show that the contribution of repeat spawners to catches can be substantial and as such the migration of kelts should be considered in the context of their likely proximity to marine renewable developments. For Scotland, there is almost no information on migratory routes or behaviour as far as the authors are aware. Data from other countries suggest rapid migration to the open sea at shallow depths (<15m).

3.0 Anadromous Brown Trout (*Salmo trutta*) – Sea Trout

Brown trout are a UK Biodiversity Action Plan (UK BAP) Priority Species (URL 2). They are the most widely distributed fish species in Scotland’s freshwater environment, exhibiting a wide range of life history strategies. Brown trout have been observed to live locally in running freshwaters for the entirety of their lives (resident), or to migrate to lochs, large rivers, estuaries (slob trout) or out to sea (sea trout) for part of their lives. In many cases a range of life history strategies can be observed within the same fish population (e.g. Jonsson, 1985). Although the mechanisms controlling trout migration and anadromy are not fully understood, it is thought that genetics (Jonsson, 1982; Ferguson, 2006) and environment (Jonsson, 1985; Olsson, *et al.,* 2006) both play a role. In common with salmon, sea trout may spend a variable number of years in fresh water before migrating to sea, where they may spend variable periods of time before reaching maturity. In contrast to salmon, immature sea trout often return to fresh water to over-winter. On reaching maturity sea trout may spawn one or more times, normally annually (Jonsson, 1985). Fish that return to fresh water in the same year as migrating are variously known as finnock or whitling. Fish that have spent a single winter at sea are normally termed adult fish. The term post-smolt is usually used to refer to fish at sea up until the end of the first winter.

3.1 Post-Smolt Migration and Behaviour of Sea Trout

There have been few detailed studies of post-smolt marine migratory behaviour in Scotland. Pemberton (1976) studied the prevalence and abundance of sea trout in sea lochs (Feochan, Etive, Creran, Linnhe, Eil) on the west coast of Scotland between 1970 and 1971 using seine nets deployed from the shore. Sea trout post-smolts appeared in large numbers in the sea lochs between April and late June. Finnock re-appeared in the loch in late August and September. Based on these observations and the results of tagging studies, Pemberton (1976) concluded that post-smolts moved from rivers to sea lochs primarily between April and early June, moving to the open sea in late June and July, before returning in August and September. These results also indicated that, in contrast to salmon, the migratory movements of sea trout at the study sites were relatively localised.

Johnstone *et al.* (1995) carried out a manual acoustic tracking study of post-smolt migration in Loch Ewe in the north-west of Scotland. Twelve sea trout smolts, from two locations, were fitted with external acoustic tags. Three fish returned immediately to fresh water, and the remaining fish were tracked by boat for periods ranging from 1 to 68h. In general the fish appeared to use inshore littoral zones, although more extensive and directed movements were also observed. All the fish from the location in the upper Ewe remained within 1.5km of the release point during the period of monitoring. A single fish tagged further towards the seaward end of the loch moved a distance of 6km in 50h. In most cases fish swam in the top 10m (in ca. 50m of water), although deeper movements to 20m were observed. In general terms the findings of this work are in agreement with those of Pemberton in indicating localised marine habitat use during the period immediately following migration. Unfortunately, it was not possible to obtain data over a longer time period given the technology and facilities available.

Middlemas *et al.* (2009) carried out a more detailed and extended study of post-smolt movements in Loch Torridon. The study focussed on two connected sea loch basins within the wider Loch Torridon area; these were Upper Loch Torridon and Loch Shieldaig. Fish were tagged in the River Balgy (n=24) in Upper Loch Torridon and the River Shieldaig (n=24) in Loch Shieldaig between 26 April and 9 May. The locations of fish were monitored at strategic locations using logging acoustic receivers for >55 days. Of the 48 fish tagged, five left the study area to move further out to sea and two fish re-entered fresh water. In common with other studies, post-smolts were shown to disperse slowly into the marine environment in the weeks following emigration from fresh water, with only 36% of fish detected >6km from their release site.

These studies have so far been confined to the west coast of Scotland. Unfortunately, comparable tracking studies are not available for the east coast where local geography would make tracking, and particularly passive tracking (with hydro acoustic listening stations), more challenging. Consequently the only data available on post-smolt movements on the east coast come from tagging studies. In many cases uncertainty over life stage at tagging, or time between tagging and recapture, prevent understanding of movements specifically at the post-smolt stage (e.g. Nall, 1935). However, Shearer (1990) reported the findings of sea trout research conducted on the North Esk between 1971 and 1981 which identified the stage of tagging and time of recapture, thereby permitting some insights into fish movement within the first year at sea. Smolt tagging took place between 1976 and 1980. The number of smolts tagged annually varied between 1089 and 6134. Following migration to sea some finnock returned to the river as soon as 5-6 weeks later. Based on the timing of returns and the spatial distribution of recaptures Shearer (1990) concluded that most post-smolts were probably staying within a short distance of the North Esk. However, smolt recaptures in the following year (unspecified times that could include post-smolt) were observed in areas around the coast of Scotland as far north as the River Spey and as far south as the River Tweed, although the vast majority of recaptures were in the vicinity of the Esk rivers. Interestingly almost twice as many recaptures were made in the South Esk as the North Esk.

Research on the migratory movement and behaviour of sea trout post-smolts has been carried out in other countries, particularly Norway. Finstad *et al.* (2005) investigated the movements of wild sea trout post-smolts alongside hatchery reared Atlantic salmon in a Norwegian fjord. Details of the study are provided in Section 2.2 above. Fifteen sea trout smolts were tagged with acoustic tags. Only four were recorded beyond 9km from the release site. The time taken to reach 9km was on average 438h. No sea trout were recorded as far as 77km (still within the fjord) from the release site during the course of the study (May to September). Similar work was carried out by Thorstad *et al.* (2007) using wild and hatchery reared salmon smolts and wild sea trout smolts. Again the details of this study are presented in Section 2.2 above. In this case 34 sea trout smolts were tagged and released throughout May and early June. Eight and three fish were subsequently detected at 9.5 and 37km, respectively; none were detected at 65km.

Taken together, netting and tracking data for sea trout post-smolts suggest relatively local movement, often within local fjords or sea lochs for the first couple of months in the sea. The findings of the Norwegian studies are in general agreement with those from the west coast of Scotland. However, it remains unclear how post-smolts migrate and behave on the east coast of Scotland where detailed studies of the post-smolt phase are generally absent and the geography is significantly different without sea lochs or fjords.

3.2 Marine Migration and Behaviour of Adult Sea Trout

This section is primarily intended to focus on adult fish (i.e. at least 1SW) movements in the marine environment. However, the available information is not always sufficiently detailed in terms of life stage at tagging and date of recapture to ensure that some post-smolts or finnock are not included. It is also worth noting that not all fish were tagged in their river of origin, fish sometimes being tagged near rivers or in estuarine areas. As such, there is the risk that apparent patterns of movement for a particular river reflect movement of fish from several rivers.

In contrast to the detailed studies of post-smolt movement which have primarily focussed on the west coast, the majority of tagging studies have taken place on the east coast. Nall (1935) summarised the findings of known sea trout tagging studies between 1914 and 1935 and in many ways our understanding has not progressed substantially since this early summary paper. There is little value in repeating the details prepared by Nall. However a concise overall summary of the findings is probably necessary in the context of this report. Tagging studies were carried out along much of the east coast of Scotland. Locations included Beauly, Ness and Firth area (Tag n (**Tn**) = 1595 Recapture n (**Rn**) = 250), Findhorn (Tn = 481, Rn = 105), Spey (Tn = 560, Rn = 20), Ugie (Tn = 264, Rn = 25), Ythan (Tn = 933, Rn = 42), Don (Tn = 1099, Rn = 30), Forth (Tn = 300, Rn = 0) and Tweed (Tn = 596, Rn=157). Across all studies, the dominant pattern was of local recaptures (within local estuarine / river / firth area), with very few distant recaptures. In most cases distant recaptures were in adjacent rivers or nets, within 40 miles or so. However, there are also a few notable longer migrations reported. For example, fish tagged in the vicinity of the Black Isle were recaptured east of Banff (68 miles) and in the Don (125 miles). A fish tagged in the Spey was recaptured in the Ythan (80 miles); a fish caught in the Ythan was recaptured at Callander (165 miles); and fish from the Tweed were recaptured to the north in the Forth (70 miles), Tay (80 miles) and South Esk (90 miles), to the south off the coast of Norfolk (270 miles) and off the Dutch coast.

On the west coast, tagging efforts were more conservative. Fish were tagged at Loch Stack (Tn = 48, Rn = 1), Loch More (Tn = 21, Rn = 0), Loch Ewe (Tn = 77, Rn = 1), River Doon (Tn = 562, Rn = 3), Girvan (Tn = 170, Rn = 1), Stinchar (Tn = 387, Rn = 3), Annan (Tn = 10, Rn = 0), Cree (Tn = 64, Rn = 2) and Border Esk (Tn = 901, Rn = 52). In most cases the few observed recaptures were local. The Border Esk yielded the greatest number of recaptures: 22 in the Esk; 20 in the nets on the north of the Solway Firth; two on the south side of the firth; three in the Eden (Solway); and one each in the Sark (Solway), the Annan (Solway), the Urr (Solway), and the Calder (Cumbria), together with one on the Irish coast near Dublin.

On the North coast, a single tagging experiment was carried out in the Hope system (Tn = 240, Rn = 7), with all fish recaptured in the Hope system. On Orkney, fish were tagged in Graemeshall Loch, St. Mary's Loch and adjacent sea areas (Tn = 546, Rn = 134). Many of the fish were probably freshwater resident brown trout. Nevertheless, all recaptures were within 2-3 miles of tagging. Finally on South Uist fish were tagged in the Howmore system (Tn = 618, Rn = 12), Kildonan system (Tn = 182; Rn = 2) and Bharp system (Tn = 77, Rn = 2). All, except a single recapture, were made in the system of tagging.

Although these early studies showed that the vast majority of fish were recaptured close to the point of tagging, Nall (1935) warned against drawing over simplistic conclusions of locally constrained movement. Specifically, Nall (1935) identified that the fish were often tagged and therefore recaptured in local sweep nets, that their likelihood of recapture at sea would be low compared with the river and that coastal bag nets were generally ineffective in capturing sea trout.

More detailed information on sea trout movements is available for the Montrose area (Nall, 1935; Shearer, 1990) and for the Tweed where Ronald Campbell (pers. comm.) has summarised the recapture data from a large number of previous studies. Sea trout tagging was first carried out in the Montrose area in 1933 and 1934. Sea trout of various ages were tagged as part of the study (Tn = 2567, Rn = 396). This included fish tagged at the Bervie (Tn = 187), North Esk (Tn = 940) and South Esk (1440). In common with other studies a high percentage (85%) of fish were recaptured close to the tagging sites (within five miles). Once these local recaptures are excluded, the broader pattern of recaptures is shown in Figure 18. Of the seventeen Bervie fish that were recaptured, seven were recaptured in Bervie Bay, one in the River Bervie. Of the remaining fish, eight moved south as far as the Forth (90 miles) and one moved north as far as the Beauly (175 miles). From the North Esk tagging, there were 149 recaptures, 50 in the North Esk, 11 in the adjacent area of sea, 58 in the South Esk, one in coastal nets, one in the Lunan Water, seven in the Tay and two in the Forth. From the South Esk tagging there were 230 recaptures. The full distribution is shown in Figure 18. In brief 155 fish were recaptured in the river or nearby nets, 25 moved south as far as Craster in Northumberland and Dogger Bank (190 miles east of Hartlepool), and 46 moved north as far as the Deveron. Given the variable time of tagging and recapture, the variable life stage of tagging and the unknown intermediate movements, it is not possible to ascertain the exact movements of the sea trout from these tagging efforts. However, the broad overall distribution and use of adjacent rivers suggests a complicated and individually variable pattern of migration.

Shearer (1990) reported the findings of later tagging studies also at Montrose. The findings of the sea trout smolt tagging were referred to in Section 3.1 above. However, the studies also included information on smolts recaptured more than one year after migration and tagging of finnock and adult sea trout. For tagging at all life stages, the majority of recaptures were in the North Esk and adjacent South Esk.

Rates of recapture declined with distance north and south outside of these areas. Smolt recaptures were obtained as far north as the Spey and as far south as the Northumberland coast. Finnock were recaptured as far north as the Spey and as far south as the Tweed. Adult fish were caught as far away as Lewis, Denmark and the Swedish coast. The findings of Shearer (1990) were in general agreement with Nall (1935), with the addition of substantial long distance migrations in some cases.

The Tweed has long been the focus of sea trout studies. Recently Ronald Campbell of the Tweed Foundation combined the results of tagging studies between 1852 and the present (Ronald Campbell, pers. comm.). The distribution of recaptures from these studies around the UK coast is shown in Figure 19. While the majority of recaptures are again around the Tweed, it is also evident that Tweed sea trout can be wide ranging, with recaptures from Aberdeenshire to the south west coast of England. Substantial numbers of Tweed sea trout have also been caught around the Dutch, German and Danish coasts

There have been no studies of the swimming depths used by sea trout in Scottish coastal waters. However, information is available from a single study conducted in Norway (Rikardsen *et al.,* 2007). Eight sea trout were tagged with data storage tags on their migration out of freshwater and re-caught 1-40 days later in coastal bag nets or the local fish trap. Data recovered from the DSTs showed that they were located at a mean depth of 1.8m and spent 93% of their time at <3m during the time between tagging and recapture. Despite the generally shallow swimming depths, frequent dives were observed to depths of up to 28m.

In summary, it is hard to determine common patterns of migratory movement or behaviour, either in general or for particular rivers. On the west coast it appears that many sea trout may use locally constrained areas. However, the reported rates of recapture and the opportunities for recapture are very limited outside of the river of origin. Consequently it is possible that this apparent pattern of local habitat use is in fact an artefact of available data. On the east coast it is clear that fish exhibit wide ranging migrations. Sea trout have also been caught by fishing vessels in Scotland’s seas (Nall, 1937) suggesting that offshore movement and migrations are also a feature of sea trout behaviour. Given the data available to date, no reliable conclusions can be drawn as to the marine distribution of adult sea trout. There is limited information on swimming depths for adult sea trout. However, available data suggest generally shallow swimming depths (<3m) with frequent dives to depths of up to ca. 30m.

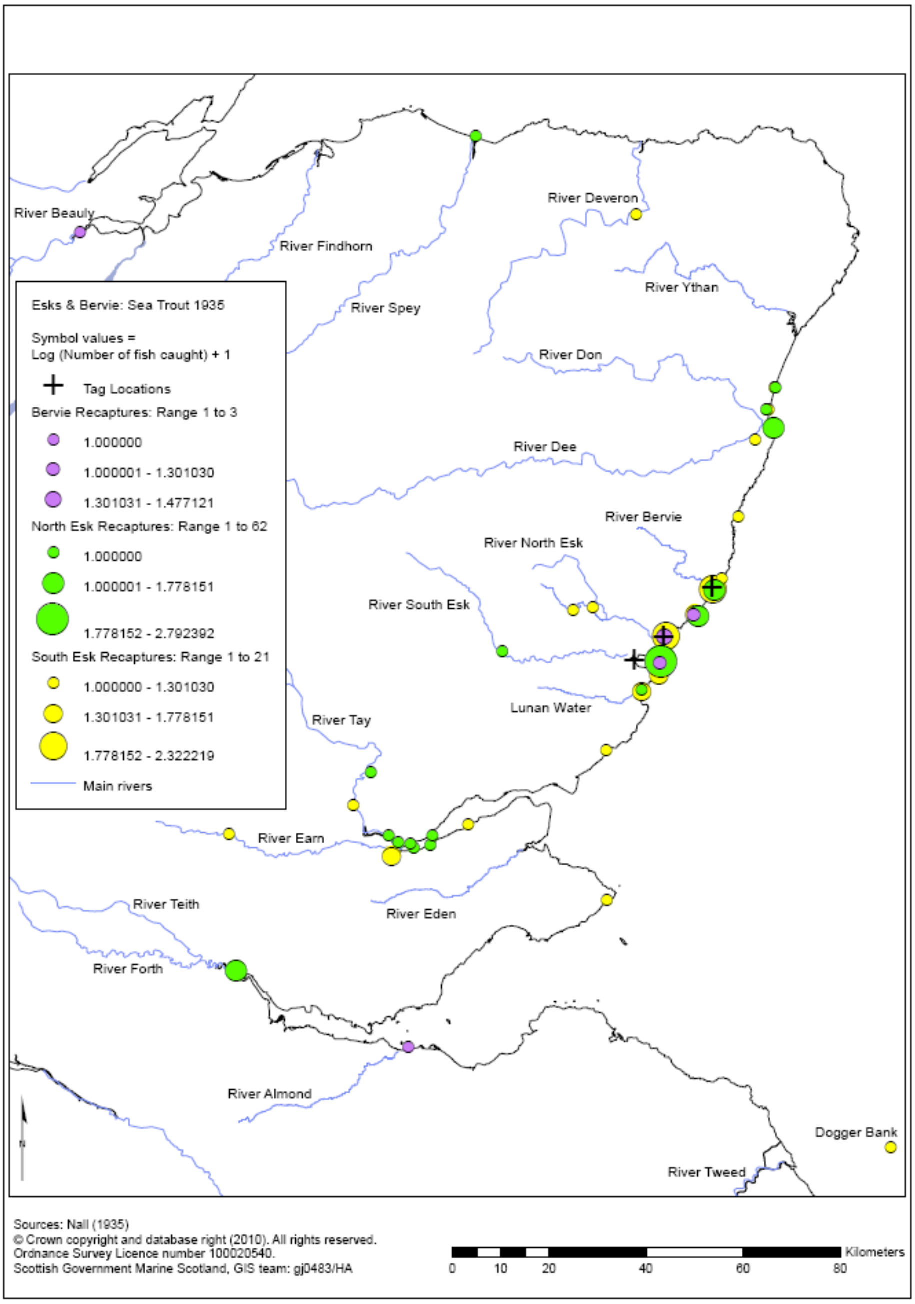

Figure 18 Map showing the distribution of sea trout recapture locations from tagging programmes in the rivers North Esk, South Esk and Bervie.

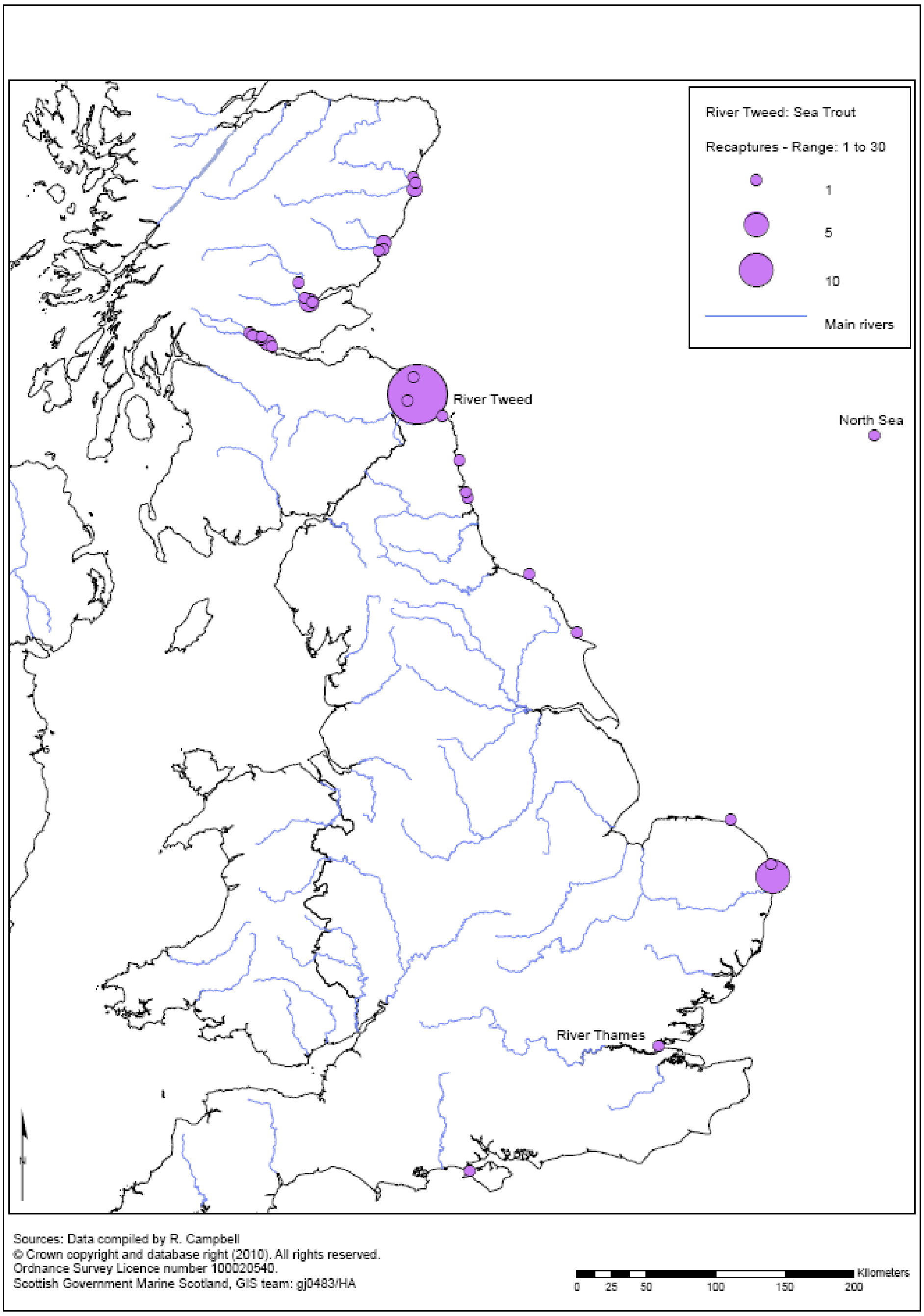

Figure 19 Map showing the distribution of sea trout recapture locations from a compilation of tagging programmes on the River Tweed (Ronald Campbell, pers. comm.).

4.0 European Eel (*Anguilla anguilla*)

The current range of the European eel encompasses almost the entire seaboard of Europe, stretching from the Arctic Circle to Northern Africa, including Baltic and Mediterranean coasts, and penetrates far into the interior of the continent (Dekker 2003). In contrast to salmon, eels are regarded as a panmictic (i.e. single stock) population with no coherent genetic structure across their range (ICES 2009).

Accordingly the population needs to be understood and managed as a single entity, since adults from all areas of Europe potentially contribute to the future population of all other parts of Europe.

Recruitment of juvenile eels to the European stock is presently at about 5% of levels that pertained in the 1970s (ICES 2009). This collapse threatens aquatic biodiversity and the socio-economic value of eel fisheries throughout its range. The problem is internationally recognized as a conservation priority: the International Union for Conservation of Nature (IUCN) assessed the European eel as ‘critically endangered’; the species is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); and the International Council for the Exploration of the Seas (ICES) have pronounced the stock as being outside safe biological limits (ICES, 2000 and subsequent reports). Within the UK it is listed as a Biodiversity Action Plan species. In 2007 an EU Regulation establishing measures for the recovery of the stock of the European eel (1100/2007) was enacted, requiring Member States to produce eel management plans, principally to reduce anthropogenic mortality of eels to a level that allows at least 40% of the natural spawner escapement biomass.

In outline the life-cycle of the European eel is well known. Based on the distribution and size of eel larvae caught in Atlantic trawls, (Schmidt 1923, Schoth & Tesch 1982) spawning is thought to occur in the vicinity of the Sargasso Sea (Fig. 3), though it has never been observed directly. Larval eels cross the Atlantic Ocean and by the time they reach the continental shelf of Europe metamorphose into un-pigmented “glass” eels, at around 5cm in length. Some of these glass eels remain in the sea, some ascend the rivers of Europe, and others may move back and forth between marine, estuarine and freshwater environments. All eventually develop pigmentation, and are generally thereafter known as “yellow” eels. After a continental growth stage which can last from 3-60 years depending on environmental conditions, the yellow eels metamorphose into “silver” eels and begin the return migration to the spawning grounds (Tesch 2003). Males generally mature faster and at a smaller size than females, which may measure up to one metre in length.

Thus the European eel undergoes two distinct migratory movements, juvenile and adult, which are dealt with separately below. Relatively little is known about the route or nature of either migration. However, for both migrations it is possible that a significant proportion of the total European population may pass through the seas around Scotland. In addition to the two migrations, marine resident yellow eels are likely to inhabit the coastal areas of Scotland, but neither their number nor their movements are known.

4.1 Juvenile Eel - Migration Routes

No direct accounts of larval migration routes are available, and the larval ocean migration remains one of the most controversial aspects of eel biology. Cohort analyses (Schmidt 1923) suggested that two years were taken by larvae to cross the Atlantic. Subsequent measures of otolith microstructure, however, have generated estimates of the time taken to cross the Atlantic to be less than one year (Lecomte-Finiger 1992, 1994). To account for such a short crossing time has necessitated the proposal of models of larval eel transport which involve active swimming (Tesch 2003). However, since the calculated swimming speeds necessary to achieve a rapid crossing are unrealistically rapid (McCleave *et al* 1998, Bonhommeau *et al* 2009a) it appears more likely that glass eels approach the continental shelf of Europe via passive migration in the Gulf Stream and on the North Atlantic Drift (NAD), the principal current of the North Atlantic (Fig. 3).

Standard schematic representations of the North Atlantic currents suggest that the north west, north and eastern coasts of the UK are close to the major currents, with the north west in particular being close to the NAD (Fig. 3). The NAD forks to the west of Shetland, with the south fork passing between Shetland and Orkney, leading to the North and Baltic Seas, while the north fork passes to the north of Shetland to form the Norwegian current (Fig. 3, URL 3)

Simulation modelling of larval eel drift in the Sargasso Sea, incorporating mortality, and terminating at 20ºW suggests that peak arrival density of larval eels is likely to be in the latitudinal range corresponding to France and the British Isles (see Fig 2 in Bonhommeau *et al* 2009b). Eels are expected to arrive in greatest numbers in the strongest currents, because eels in slower currents have lower survival to continent rates. Potentially, therefore, a significant proportion of juvenile eels arriving in Europe, particularly northern Europe, may pass through the vicinity of western and northern Scotland by which time they will be glass eels rather than larvae.

There are no known data on trawls of glass eels in the seas off Scotland, and the only information that can be brought to bear is indirect evidence from the standing stocks of eels in fresh water. Such data have been collected in Scotland by the Scottish Fisheries Co-ordination Centre (SFCC) from 1997 to 2006 and analysed for the Scotland River Basin District Eel Management Plan (URL 4). In general they support the view that proximity to Atlantic currents is associated with high eel numbers, with greater ubiquity and higher densities of eels being reported in the rivers of the Outer Hebrides, north west and northern coasts of mainland Scotland. (Fig. 20 & 21). It should be noted that eels were not the target species during the collection of these data, and it is likely that they were generally under-reported. No data were available for Orkney or Shetland.

In more detail, the south fork of the NAD that enters the North Sea appears to be itself composed of further currents, of which three main currents are recognised: The Fair Isle Current (an easterly flow between Orkney and Shetland); the East Shetland Inflow (passing north of Shetland, then skirting its eastern shores); and a southerly current along the western edge of the Norwegian Trench (Fig. 22, Turrell *et al* 1996, Holliday & Reid 2001).

There is little indication of non-passive glass eel migration on arrival at the continental shelf and accordingly the most likely migration routes therefore follow ocean currents. Flux into the North Sea via the English Channel has been estimated as ~15 $x10^4$ $m^{-3}s^{-1}$ (Bailly du Bois *et al* 1995), approximately an order of magnitude lower than the estimated flux of combined northern currents into the North Sea, estimated at ~162 $x10^4$ $m^{-3}s^{-1}$ (Turrell *et al* 1992). This northerly flow was dominated by the Norwegian Trench current (~102 $x10^4$ $m^{-3}s^{-1}$), while the Fair Isle Current flux accounted for ~20 $x10^4$ $m^{-3}s^{-1}$, and the East Shetland Current for ~40 $x10^4$ $m^{-3}s^{-1}$. If glass eel arrival can be regarded as essentially passive then these current fluxes may approximate to the proportions of glass eel arriving in north west Europe. Therefore the Fair Isle Current may carry in the region of 10%, and the East Shetland Current about 20% of the entire glass eel migration to north west Europe, including the Baltic and the east coast of the UK.

The assumption that glass eels follow the course of prevailing currents may be over-simplistic. Even where surface currents are described, these may not accord well with the movement of eels situated at different depths. In addition the strength of different currents varies seasonally and on decadal scales (Turrell, 1992; Dulvy *et al.* 2008). Relatively warm temperatures are found in the NW North Sea particularly during positive North Atlantic Oscillation (NAO) phases, when persistent westerly winds in the North Atlantic result in stronger inflow of warmer North Atlantic waters (Svendson *et al* 1995, Edwards *et al* 2002). For this reason many warm water species have first arrived in the North Sea from the north rather than the south (Ehrich & Stransky 2001). This suggests that the proportion of glass eels reaching North Western Europe via migration routes to the north of the British Isles as opposed to the English Channel may vary with short-scale variation in NAO. However, while the wintertime inflow of the Fair Isle Current has been shown to be positively correlated with NAO, the wintertime inflow in the East Shetland current is negatively correlated with NAO (Planque & Taylor 1998), and glass eel arrival in the Shetland area is likely to peak in early winter (Tesch 2003, see below). The circulation of the North Sea is difficult to determine, but it seems that inflows from the North and South are largely independent of each other (Becker & Pauly 1996).

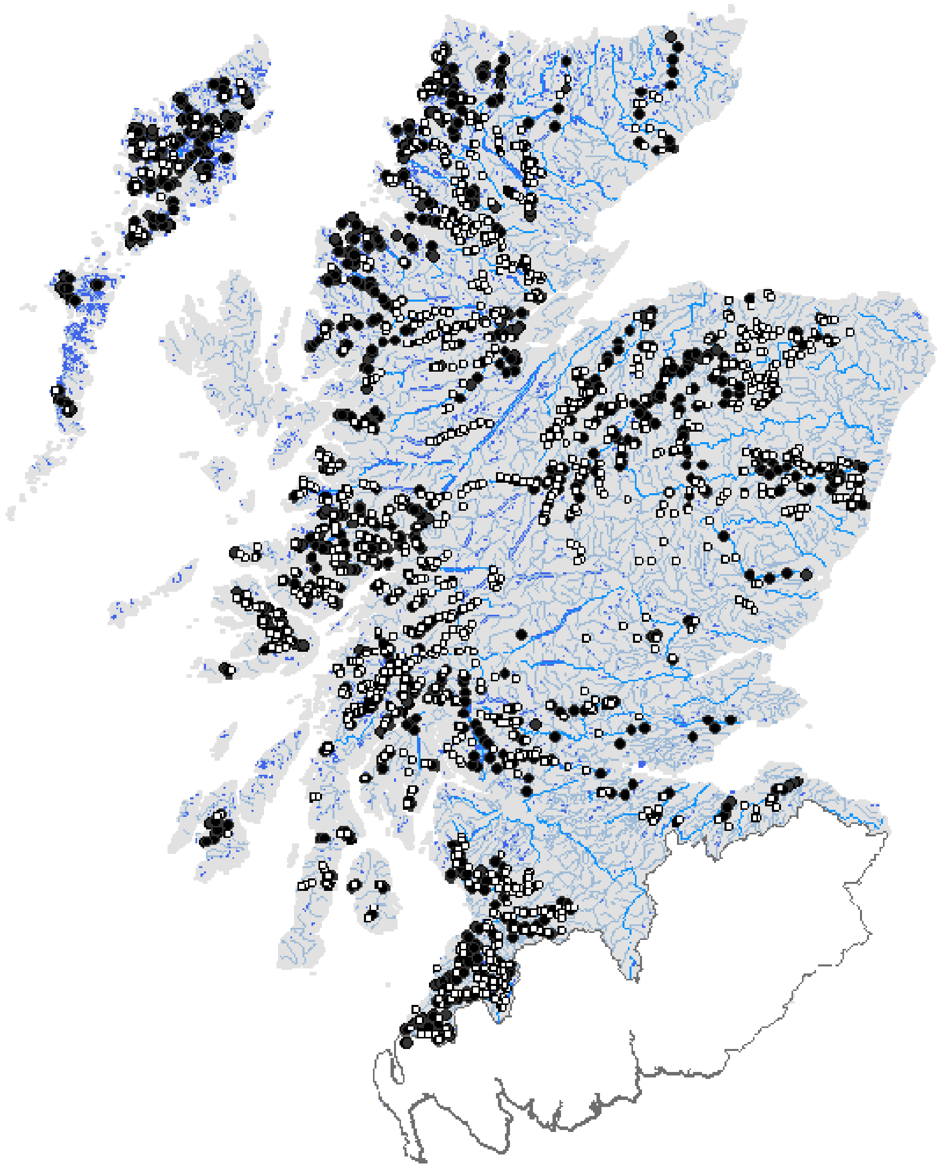

Figure 20. Eel presence (●) or absence (◦) for sites electrofished in Scotland RBD between 1996 and 2006. Where sites were visited more than once, eels appear as present if they were reported at the site on any occasion. Source: Scottish Fisheries Coordination Centre. It should be noted that eels were not the target species during the collection of these data, and as such it is likely that eels were generally under-reported. No data were available for Orkney or Shetland.

No major net current through the Pentland Firth is recognised, but there is evidence to suggest that the area is nevertheless widely used at least by those eels which colonise the eastern seaboard of Scotland. Data presented in Figures 20 & 21 indicate very high probabilities of encountering eels in rivers in north western

Scotland, high probabilities on the north coast rivers, low probabilities in the rivers of the inner Moray Firth, and moderate probabilities along the rest of the east coast of Scotland. This is consistent with a significant eastward migration of glass eels through the Pentland Firth, and seems unlikely to result solely from migration via the Fair Isle Current.

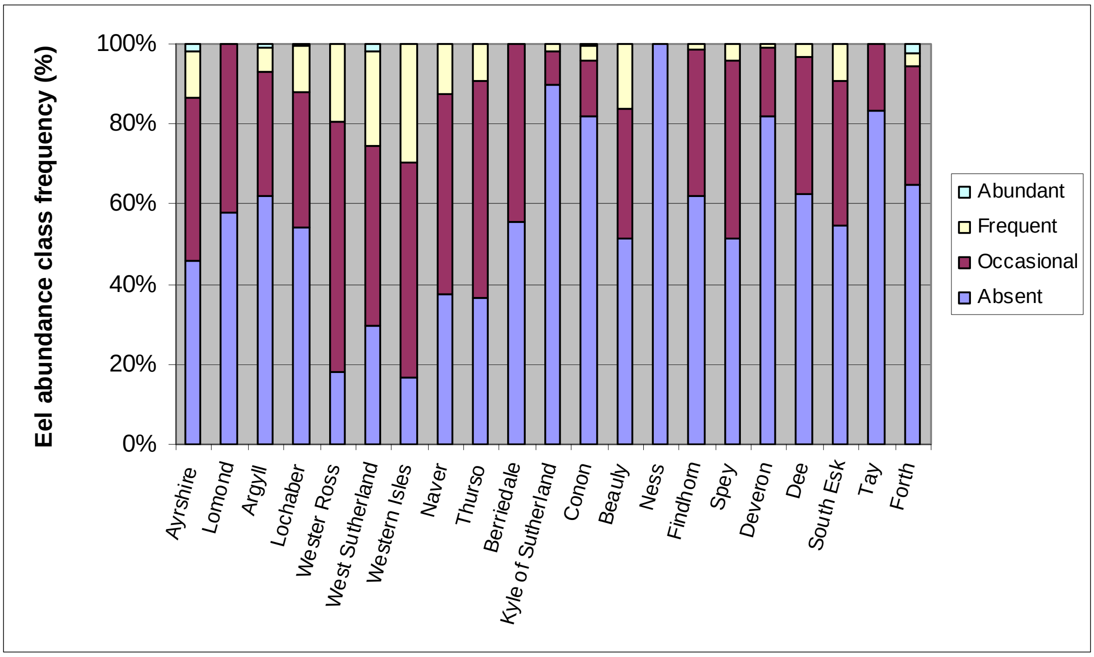

Figure 21. Percentage frequency of eel abundance class at electrofishing sites in various rivers or districts of Scotland RBD. Areas are arranged clockwise around the coast, from Ayrshire in the south-west, to Naver and Thurso on the north coast then down the east coast to the Forth region. Where more than one visit to a site was made the highest recorded abundance class was used. In general eels were more widely distributed and more common in the north-west and north. Source: Scottish Fisheries Coordination Centre.

Such eels may be carried in a coastal current flowing north up the west coast, then east along the north coast of Scotland, although the major Scottish Coastal Current appears likely to circulate north through the Minch, then west and south down the west coast of the Outer Hebrides (Hill *et al* 1997). Coastal currents may be seasonal in nature, and potentially can be dominated by wind, particularly when stratification breaks down in the early autumn (e.g. Fernand *et al* 2006). Accordingly it should be assumed that migrating glass eels may be found in all the seas around Scotland, though perhaps in greatest numbers around north and west Scotland, and that there may be high concentrations in particular, but as yet unknown, areas. In the absence of additional information it is not possible to quantify, or even reliably estimate, the likely scale of glass eel migration in the coastal zones of Scotland.

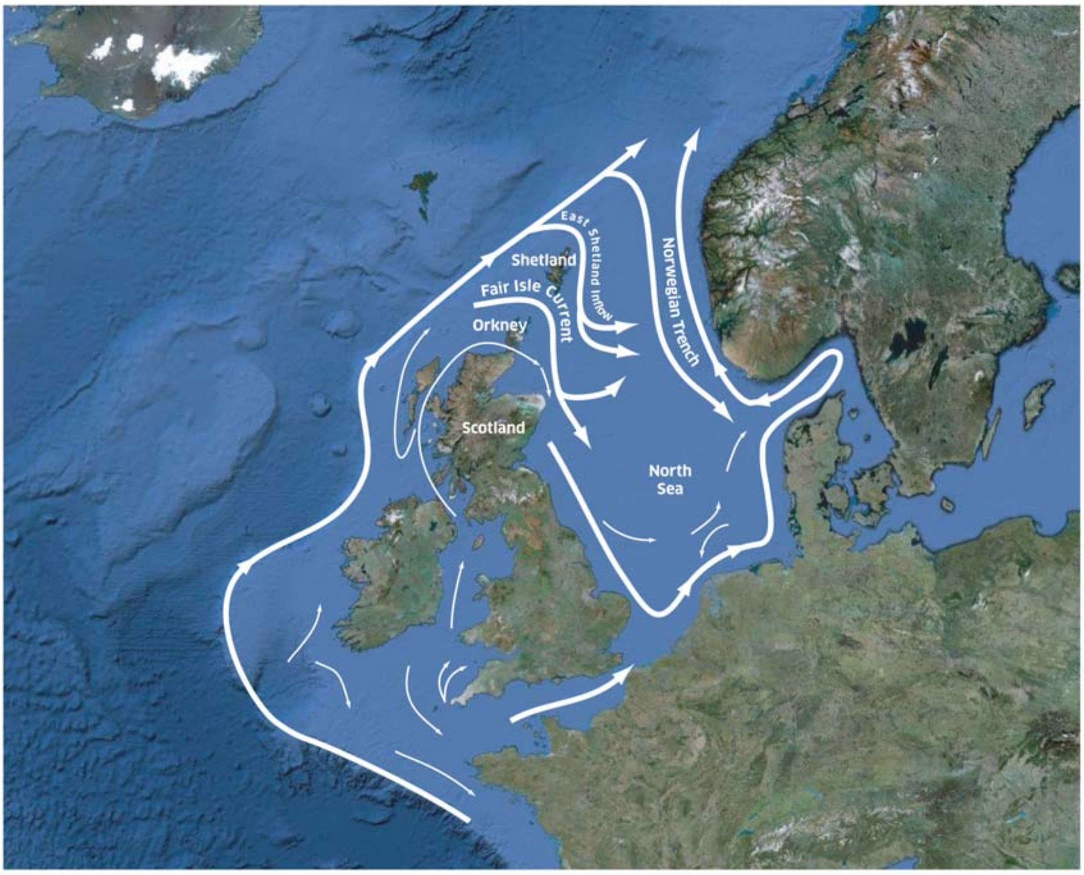

Figure 22 Ocean currents in the vicinity of the British Isles. Background image ©2010 Google - Imagery ©2010 TerraMetrics, NASA

4.2 Juvenile Eel – Migration Timing

The arrival of glass eels in the seas around Europe is seasonal, and varies spatially. According to Tesch (2003) eels typically arrive earliest in the north and west, arriving typically off Shetland and the Western Isles in September, Orkney and Caithness in November, and rest of eastern mainland Scotland in December. However the first eels may arrive as early as August, and continued arrival of glass eels is likely to occur for several months after the mid-winter peak, perhaps even through the whole year in lower numbers. Based on reported arrival times of glass eel at various points Creutzberg (1961) inferred that the progress from the north to the south of the North Sea proceeded at around 7km/day. Glass eels may migrate into fresh water in their first year after arrival, though some may remain in coastal waters until they mature, while others may move back and forth between coastal, estuarine and freshwaters throughout their lives (Daverat *et al* 2006). Movement of eels into freshwaters shows considerable seasonality, being governed principally by water temperature (Tongiorgi *et al* 1986, White & Knights 1997, Edeline *et al* 2006). Freshwater temperatures rising to12-14º C are associated with increased upstream movements, though river flows may also be important (Acou *et al* 2009).

4.3 Juvenile Eels – Migratory Behaviour

All juvenile eels found in the shallower waters off Scotland are likely to be glass eels, with larval eels occurring only to the west of the continental shelf (Tesch 2003). Accordingly amongst juveniles we concentrate on the known migratory behaviour of glass eels.

Creutzberg (1961) inferred glass eel progress rates in the North Sea from arrival times at different locations, and found that these movement rates agreed well with reported residual north-easterly flow in the region, leading to the conclusion that glass eel migration in the open sea was essentially passive. While Tesch (2003) expressed concerns that this conclusion was inconsistent with the glass eel's "primarily active manner of propulsion" (in contrast to larval eels), no data are available that support active migration in the horizontal plane. Conversely, active vertical movement has been widely observed, and is used by glass eels to exploit tides, at least during movements on shore. Tidal currents are likely to be weak in deep water, but in shallower coastal zones progress made by use of tides can be significant. For example, in the tidal Texel Current in the Netherlands, studies using plankton nets in 8m of water has shown that during flood tides glass eels favour parts of the water column near the surface, thus favouring movement toward the coast, while often lying on the sea-bed, where current is minimal, during ebb tides (Creutzberg 1961, Tesch 2003), so avoiding being drawn back out to sea. Daylight suppresses this behaviour, even full moonlight being sufficient to drive glass eels away from the surface (De Casamajor *et al* 1999).

In captivity, glass eels of the related species *Anguilla japonica* show similar behaviour with greater activity levels in darkness than in daylight (Dou & Tsukamoto 2007), suggesting that active migration is likely to be principally nocturnal. Artificially reared glass eels show a benthic distribution in light conditions, but a random vertical distribution in darkness (Yamada *et al* 2009). Similar patterns of behaviour are expressed in the larval stage of *A. anguilla*, with larval distribution ranging from ca 300m during daylight, to near-surface during the day (Castonguay & McCleave 1987). The avoidance of light is generally regarded as an anti-predator behaviour in both larval and glass eel (Tesch 2003).

4.4 Adult Eels – Migration Routes

Although the onset of the spawning migration in rivers is well-documented, very little is known about the sea phase of the spawning migration. Eels from the east coast of the UK, together with eels from Scandinavia, the Baltic, and the Low Countries have a choice of two major routes to reach the breeding grounds: via the English Channel or via the north of Scotland. It appears highly unlikely that eels from further south or east in Europe select a route that passes round the north of Scotland. Eels from western Scotland may have a direct ocean route to their breeding grounds, but eels leaving south west Scotland, Wales and western England again face the option to pass north or south around Ireland.

There is no information on the migration of eels from the west of Great Britain, so no conclusions can be reached on the use of routes via the north or south of Ireland. Eels tracked using pop-off tags leaving the west coast of Ireland were found to head in a southwest direction, suggesting use of the Canary Current and North Equatorial Drift (see Figure 3) rather than a direct line to the Sargasso Sea (Aarestrup *et al* 2009), but whether eels leaving north-western Scotland behave in a similar matter remains a matter of speculation.

A large body of work has been conducted on the migratory movements of eels within the Baltic Sea (references in Tesch 2003), but these have little or no bearing on the movements of eels around the seas off Britain, since all (successful) eels must eventually escape the Baltic from its single mouth. Accordingly these studies are not reviewed here, except in so far as they relate to behaviour that may be more generally applicable. Unfortunately direct observations of migrating adult eels outwith the Baltic are limited, but those that are available provide some support for preference of the route via the north of Scotland. Tesch (1974) tracked eels in the North Sea and found a mean direction of travel of 341º amongst silver eels, whereas yellow eels tracked at the same time were mostly heading in a south-easterly direction. Further studies by (Tesch 1992) appear to confirm the northerly direction choice by other eels in the North Sea near the Helgoland. By contrast, when tracking eels for a short period (<24hours) off the continental shelf in the Bay of Biscay region, Tesch (1978) found eels tracked roughly west (288º), close to a direct compass bearing for the putative breeding grounds in Sargasso Sea area. In general Tesch's work supports the view that eels migrating from the Baltic and the western North Sea take a migration route that passes to the north of the British Isles.

Evidence for migration routes of eels leaving the east coast of Britain is scant and equivocal. McCleave & Arnold (1999) tracked 10 silver eels (obtained from "various locations in England") for up to 58hrs during the autumn migration period off the east coast of England (from Humber to Lowestoft) and found silver eels heading in all offshore directions in approximately equal numbers. Two silver eels oriented onshore. Two eels sourced from Scotland were also tracked, one oriented NE, the other SE, but neither was tracked during the migratory period. This study therefore does not provide evidence to support either a northerly (via north Scotland) or a southerly route (via the English channel), but perhaps suggests that eels from eastern England may adopt either strategy, or simply that eels in the period of a day or two after their release are not actively migrating to the breeding grounds. The four yellow eels in the same experiment all exhibited on shore movements. It would therefore appear that silver eels do not tend to hug the British coast on migration. Experiments examining orientation behaviour following significant translocation may however be uninformative about true migration behaviour if the process by which eels find their way back to their breeding grounds is wholly or partly governed by retracing their incoming route as glass eels.

As yet unpublished data from Kim Aarestrup and co-workers on the 'Eeliad project' (URL5) using data storage tags has provided evidence of the route of a single eel leaving the west Swedish coast at the mouth of the Baltic. The route taken by the eel followed the Norwegian Current up the Norwegian coast, before heading west to reach the Atlantic via the Shetland-Faroe channel (David Righton, CEFAS, pers. comm.). Details of the route taken were inferred from temperature, pressure and light data stored by the tag, rather than by direct positional data. The eel was eventually predated at an uncertain geographical location. There has also been a report of a single eel incidentally caught in the Atlantic Ocean to the northeast of the Faroes (Ernst 1977), perhaps providing support for a route passing to the north of Shetland.

Save for the evidence of a single eel, which was tracked passing to the north Shetland, and of a second caught to the northeast of the Faroes, there is no knowledge of the route(s) taken to access the Atlantic from the North Sea. There is conflicting evidence regarding the use of sea currents and tides by adult eels (see below), but it seems likely that selection pressure would be strong for eels to minimise energy use during migration, thus maximising energy available for reproduction in the breeding grounds. This is particularly the case because eels are not thought to feed during their ocean migration (Chow *et al* 2010). It may therefore be reasonable to assume that adult eels are unlikely to swim directly into the major currents flowing into the North Sea. Thus routes to the north of Shetland seem plausible, but equally the Pentland Firth may offer an energy efficient route, given the absence of a major contrary current and the reduced total migration distance it would entail.

4.5 Adult Eels – Migration Timing

Eels undergo an 'autumn migration' but individuals may begin to leave the rivers at almost any point of the year, with much variation between peak migration periods at particular sites. Across northern mainland Europe generally August to October peaks in migration rates are reported (Tesch 2003). Some spring migrations of silver eels in the Baltic occur, and recent studies suggest that such eels have a residency period in the immediate coastal area (Aarestrup *et al* 2008). Eels leaving two nearby sites in small catchments of the upper Dee, Scotland, begin to depart in June, peak in August or September and continue into October or even November, while on the west coast the peak month of migration at the mouth of the Shieldaig is October (Marine Scotland Science, unpublished data). A large proportion of the variation in the timing of migration in individual years on individual rivers may be affected by temperature (Vøllestad *et al* 1986), or by rainfall or the lunar cycle (Lowe 1952). Accordingly, it might prove possible to predict the timing of peak passage of adult eels in an area of sea likely to be the route for eels leaving particular river mouths.

However, it is unlikely that general models could usefully predict migration peaks in sea areas that may have migrants composed of eels from many different areas of Europe (for example the north coast of Scotland). This is because of the wide climatic difference across all the rivers of NW Europe that might contribute to migrants.

Large female eels are generally observed to contribute to the later part of the fresh water migration, and are almost absent from the earlier period (Tesch 2003). This partial separation of male and female migration from fresh water may be continued in the ocean phase, as optimum depths and temperatures during ocean migration may differ between the sexes (Sciaon e*t al* 2008). Reports of silver eel catches in open sea have been collected by Tesch (2003), and almost all catches in the North Sea and the Kattegat were between October and December, while catches in the North Atlantic were somewhat later (between late November and January). These data suggest that the period in which the majority of eels pass through a particular stretch of ocean may be more seasonal and less variable than the somewhat attenuated egress from rivers. The data also suggest that the timing of the freshwater migration may reflect the geographical location of the migration monitoring points, and the swimming speed of the individuals, in a manner that leads to a concentrated arrival at the spawning grounds. For example, the seasonal departure of eels from western Ireland, some 2000 km closer to the Sargasso Sea region than the Baltic, tends to extend later in the year. The fishing season for silver eels on the Killaloe weir, River Shannon, lasts from September to late March with main migrations in November-December (Cullen & McCarthy 2000, McCarthy *et al* 2008). However, at least one other catchment on the west of Ireland, the Burrishoole, has silver eel departure peaks in October (Poole *et al* 1990), comparable to those observed much further east.

In the absence of alternative evidence it is reasonable to suppose that the bulk of those adult eels migrating to the north of Scotland may do so between October and January.

4.6 Adult Eels - Migratory Behaviour

It is well-established that silver eels in river fisheries are caught in greatest abundance during the last quarter of the moon, although river flow is probably of over-riding importance (references in Tesch 2003). The relationship between lunar phase and eel activity applies not only in rivers and estuaries, but in the open sea. For example, studies off the Swedish coast showed greater movement by silver eel in the period before full moon than after it (Lindroth 1979, cited in Tesch).

Silver eels are known to be able to exploit tidal currents to facilitate seaward movement in the lower rivers: according to Tesch (2003) for example stow nets in

North Sea estuaries only catch eels during the ebb tide. Parker & McCleave (1997) have also shown the importance of ebb tides in lower rivers for migrating silver American eel *Anguilla rostrata.* Information regarding the selective use of tidal stream transport in the open sea is rather mixed, however, with Tesch (1974, 1992) concluding it was not used by any of the eels he tagged in the Baltic and North Sea, but McCleave & Arnold (1999) finding evidence for its use amongst a proportion of silver eels.

The depths selected by eels in shallow seas have been reported by several authors. Tesch (1992) found eels swimming at depths of 1-17m (average around 10m depth) in North Sea, where water depth was around 36m. Eels spent very little time on the sea bed. Tesch suggested that the full extent of the water column was not used due to water below the thermocline being too cold (8ºC).

In the Baltic various tracking studies have estimated habitual depths used by eels. Tesch (1979) reported eels swimming at a depth of around 25m during the day and 20m at night in water of about 50m depth in the western Baltic. Tesch *et al* (1991) reported eels generally occupying depths of around 8-15m in 60m of water off the eastern Swedish coast, while Westerberg (1979) found eels at 12-30m at night and at the sea bed during the day, in 60m of water at Bornholm off the south Swedish coast. By contrast, Westerberg *et al* (2007) reported that female silver eels in the Baltic generally rested on the sea bed at depths from 2-36m during daylight, became active from dusk till dawn and were found actively swimming during darkness, with 95% of swimming time spent within 0.5m of the surface. The available evidence does not allow confident prediction of the depths that eels might use during migration in Scottish coastal waters or further offshore, and no depth could be regarded as unlikely to be used by eels.

When deeper water is available, eels make use of much greater depths. Off the continental shelf in Biscay eels were sometimes observed near the surface at night, but swam at a mean around 150m, with most diving to greater depths (400m) at dawn (Tesch 1978). In the Western Mediterranean swimming depths averaged 196m during daylight and 344m during darkness, with maximum depths of almost 700m (Tesch 1989). Aarestrup *et al* (2009) found European eel released from Ireland swimming of the continental shelf selected much deeper water when it was available. During the night 14 eels selected relatively shallow, warm water (depth 282±138m, temperature 11.7±0.5ºC). At dawn however eels made a steep dive and spent the day in cooler deep water (depth 564±125m, temperature 10.1±0.9ºC). Temperature may play a crucial role in depth selection: Jellyman and Tsukamoto (2005) found that the Longfin eel of New Zealand (*Anguilla diffenbachii*), diving to depths of up to 980m but more frequently in 150-200m of water, often spent time at 5-6ºC. Selection of cool water has been suggested to be related to the need to delay the onset of gonadal development (Aarestrup *et al* 2009). Similarly depth, or pressure, itself may be important: swimming efficiency, assessed in terms of oxygen consumption for a given swimming speed, has been shown to increase with increasing hydrostatic pressure (Sebert *et al* 2009). Based on whole animal efficiency Sciaon *et al* (2008) suggest possible divergence of migration strategies with males favouring deep and cold water and females warm surface waters. Since most tracking studies of silver eels in the North Sea area have been conducted with female eels, due to their larger size, the possibility that males adopt different depths and even take different migration routes cannot be disregarded.

There is some evidence that heavy infection with the swimbladder parasite of the eel (*Anguillicoloides crassus*), introduced to Europe in the 1980's from the Japanese eel (*Anguilla japonica*) and now widespread, may modify eel migratory behaviour. Sjöberg *et al* (2009) found that heavily infected individuals were more likely to be caught in pound nets, and while swimming speed was not affected, distance travelled was lower for infected eels. Sjöberg *et al* (2009) speculated that the infection and subsequent damage to the swimbladder disrupted vertical migrations and caused eels to swim in shallower, onshore waters.

The foregoing paragraphs indicate that most aspects of silver eel migratory behaviour in the open sea cannot at present be reliably predicted. Eels may or may not use tidal transport to facilitate their movements, so they cannot be expected only to swim in tides which expedite their progress towards their ultimate destination. In the Atlantic migrating eels generally adopt depths below 100m, but in shallower inshore waters eels may be assumed to be found at almost any level in the water column, excepting the surface, and are not strongly associated with any particular depth.

5.0 Summary

5.1 Atlantic Salmon

Studies from Norway indicate that post-smolts travel rapidly out of fjord areas, generally at shallow depths (<10m). To date, there have been no similar studies in Scotland to determine if these observations are consistent in a Scottish context, although there is no reason to believe that they would not be. Scottish post-smolts migrate to areas to the north and west of Scotland. The exact route taken by Scottish post-smolts is unknown, although high densities of post-smolts have been observed off the west and north west coasts of Scotland. There is no information for the east coast where there are no surface trawl data.

MSW salmon migrate to areas that include the coast of West Greenland and the area around Faroe. The exact spatial distribution of migrating fish is currently unknown given the geographically limited distribution (two points) of distant water fisheries from which to obtain information. The situation with regard to 1SW fish (grilse) is less certain as both the Faroe and West Greenland fisheries primarily exploited MSW fish. No wild Scottish salmon have been caught off the coast of Norway despite substantial fisheries indicating that this area is probably not important for Scottish salmon.

Fish return to the Scottish coast from a range of directions. However, given the known distribution of marine feeding this will have a northerly and westerly bias. It is possible that fish could return directly to the east coast of Scotland travelling between Orkney and Shetland or to the east of Shetland. However, the lack of recorded salmon fisheries on Orkney or Shetland and the lack of Scottish fish captures in Norwegian fisheries suggest that this may not be common. This aspect of the return migration requires further investigation (see below).

On reaching the Scottish coast salmon subsequently migrate towards their natal river. The wide geographic distribution of arrival location and natal rivers generates apparently variable and random directions of movement for a given location (Fig. 23). The apparent exception to this rule is for the east coast, south of Aberdeenshire, where the dominant direction of movement is clearly a northerly one. In addition, the dominant direction of movement for MSW salmon on the west coast is also a northerly and easterly one given the dominance of east coast rivers in the production of MSW fish.

The limited available information on adult swimming depths suggest that they spend most of their time in shallow water (generally 0-40m), although they can dive to substantial depths up to 280m. It has been hypothesised that these dives are related to feeding or predator avoidance. On reaching the Scottish coast, gut contents suggest that adult fish are often still feeding, particularly early in the year. The swimming depths utilised by adult fish in Scottish coastal waters remains unknown, but it could be highly variable.

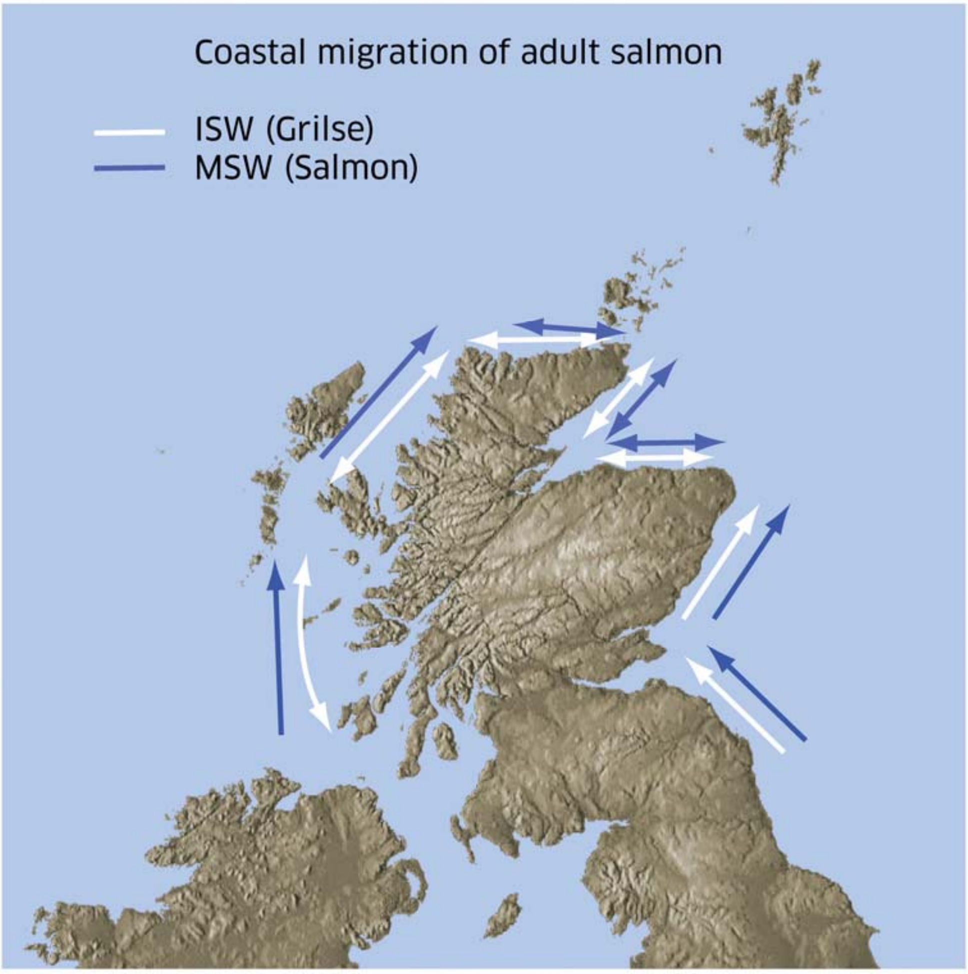

Figure 23 Dominant directions of travel for Atlantic salmon (1SW and MSW) in Scottish coastal waters based on tagging studies

5.2 Sea Trout

Brown trout exhibit a wide range of migratory behaviour that is thought to be influenced by genetics and environment. At the extreme, brown trout can migrate to the marine environment where they are known as sea trout. In contrast to salmon, sea trout post-smolts do not migrate rapidly out to sea from inshore coastal areas. Instead they tend to use near shore sea loch and fjord areas where available. It is uncertain what happens to sea trout smolts on the east coast where no such areas exist. There is relatively little information on post-smolt swimming depths although observational data generally suggests shallow swimming depths in the upper 10m or so of the water column.

Some post-smolts return to fresh water relatively quickly after migration to sea. Fish returning before their first winter at sea are known as finnock or whitling. After the first winter they are known as adults or 1SW fish. There is considerable uncertainty as to the movement of sea trout after the initial few months in the marine environment for both the west and east coasts of Scotland. Tagging data for the west coast suggest more local habitat use than for the east coast. However, this may simply reflect differences in recapture effort and opportunity. As far as the authors are aware there are no data on the swimming of depths of sea trout adults in the marine environment.

5.3 European Eel

Understanding of movements and behaviour of eels in Scottish coastal waters is limited. Potentially a significant proportion of the total European eel population, at the adult (silver eel) migratory stage, may pass through Scottish coastal waters. In particular those waters abutting the northern coast, Orkney, Shetland and the Outer Hebrides are most likely to contain migratory eels from northern continental Europe as well as the UK. However, given the paucity of data regarding adult migration (Fig. 24), it is also possible that a general migration route north out of the North Sea tracks along the Scandinavian coast and crosses into the north Atlantic to the north of Shetland, so that continental European eels may by-pass Scottish coastal waters. It is also possible that no geographically confined migration route exists.

Figure 24 Summary of the movements of silver eels observed in specific tracking studies. Presence of arrows does not imply the location of migration routes. Similarly the absence of arrows does not indicate an absence of migratory routes. Available data suggest a northerly migration from the North Sea for most silver eels leaving north west Europe. Silver eels with direct access to the Atlantic appear to adopt direct routes towards breeding grounds in the Sargasso Sea. Background image ©2010 Google - Imagery ©2010 TerraMetrics, NASA

Similarly it appears likely that a significant proportion of the European glass eel population will pass through or near Scottish coastal waters, since available knowledge indicates that ocean currents (Fig. 3, Fig. 22) are largely responsible for the distribution of the glass eel migration. It is uncertain whether the distribution of migratory glass eels in Scottish coastal waters is diffuse or concentrated in particular areas.

Both juvenile and adult migrations have a seasonal component, but in each case the season is probably quite protracted. The timing of migration peaks in Scottish waters is poorly recorded but by inference it may be assumed that glass eels pass through Scottish waters principally from September to December. In addition glass eels destined for Scottish rivers must remain in coastal regions until April or May before river temperatures rise sufficiently for them to enter fresh water. The bulk of the return silver eel migration may be deduced to extend from September to January.

Both juvenile and adult eels can be found in all levels of the water column (at least in depths of less than 300m), and the depth selected can vary with time of day and state of tide. Negative phototaxis is pronounced in eels of all stages and they are unlikely to be found within a few metres of the surface during daylight, or even bright moonlight, if deeper water is available. Glass eels travel in near-shore areas may be facilitated by moving to the sea bed in ebb tides and up into the water column in flood tides. The use of similar tactics by adult eels in open water has been observed but does not appear to be widespread.

6.0 Knowledge Gaps on Coastal Migration in the Context of Offshore Renewable Development

An understanding of the migratory routes, habitat use and behaviour of salmon, sea trout and eels in Scottish coastal waters could provide a useful screening tool for assessing environmental risk associated with marine renewable (and other) development projects. While this review has provided some indication of the issues, significant research gaps exist which are detailed below by species. Research should be commissioned to address these gaps following a prioritisation exercise between Marine Scotland and SNH and a feasibility assessment of the individual research areas.

6.1 Atlantic salmon

- There is no information on the behaviour (including swimming depths and nearshore/offshore movement) of post-smolts in the Scottish context. This is a particular issue for east coast rivers and coastal areas which differ markedly in their geography from Norwegian systems.

- There are currently no data on the migratory routes or geographical distribution of post-smolts in the North Sea.
- It is uncertain whether adults or post-smolts migrate through the area around Orkney and Shetland or if the Pentland Firth is the preferred or only route used.
- There is currently no information on the swimming depths utilised by adult fish in Scottish coastal waters.
- There is substantial uncertainty as to the mechanisms and routes by which adult salmon home to and around the Scottish coast to the proximity of their natal rivers.
- There is limited information on the timing of migration for both juvenile and adult fish for specific locations on the Scottish coast.
- The resolution of available data is insufficient to assess the likely proximity of fish to any particular projects or development areas.

6.2 Sea trout

- There is currently no detailed information on post-smolt habitat use on the east coast of Scotland where the geography is significantly different from previous studies.
- In the case of both the east and west coast adult sea trout there is very limited information on migration and feeding areas.
- There is currently no information on the swimming depths used by sea trout post-smolts or adults.
- There is limited information on the timing of migration for both juvenile and adult fish for specific locations on the Scottish coast

6.3 European eel

- Glass eel migratory routes into Scottish waters and past Scotland into the North Sea can at present only be inferred. No direct evidence is available.
- Movements of local glass eels destined for freshwater in Scotland are unknown.
- Migration routes of adult silver eels leaving northern continental Europe and the British Isles are unknown. These may pass through northern and/or western Scottish waters.
- The timing of peak migration for both glass eel and silver eel stages is poorly known in Scottish waters
- The migratory behaviour of silver eels is not well-established. In particular swimming depths and the use of tidal transport is poorly understood, and entirely unknown for Scottish waters.

7.0 Conclusions

This report has summarised the readily available information on migratory routes for salmon, sea trout and eels in the Scottish coastal environment and identified knowledge gaps as they pertain to development. In some cases further data are available which could provide additional insights, although not within the time scales of this report.

The information presented provides insights which may be useful for assessing the relative risk of renewables projects in particular areas of Scotland. However, the resolution of the available data and the risks of transferring findings between locations must be recognised as major limitations of current knowledge. In order to assess the potential impact of specific developments additional detailed local information on fish migration and behaviour, and the nature and location of the developments, would be required as identified in Section 6 above. It should be recognised that obtaining these data will not always be technologically or logistically possible depending on location and the spatial precision required.

Finally, this report has been restricted to consideration of migratory routes and behaviour of salmon, sea trout and eels. Understanding of these aspects informs assessment of potential risks of development in particular areas and in some circumstances may be overwhelmingly important (i.e. where areas can be demonstrated to be unimportant for migratory fish). However, only in the case of negative interactions between the technology deployed and the migratory fish will the potential risks be manifested in impacts. It was not in the remit of this report to identify potential impacts of different renewable technologies, but it should be recognised that an understanding of migratory routes and behaviour is only half of the information required to assess impacts through an Environmental Impact Assessment (EIA) process.

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