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Atlantic salmon: the ocean traveller

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Atlantic salmon are distributed over large areas in the North Atlantic, and the species is known to undertake long migrations. Salmon are also distributed in the Baltic, but rarely move from there into the Atlantic. More than 100 years ago, with the development of coastal salmon fisheries, detailed information on migration and distribution of the salmon in these waters started to accumulate. The knowledge of salmon movements in oceanic areas was a black box until oceanic fisheries developed in the 1960s at West Greenland and in the northern Norwegian Sea. Since that time, the information about the oceanic life history of Atlantic salmon has improved considerably. At West Greenland, salmon from Canada, the United Kingdom (UK), and Ireland are most abundant, but fish from most salmon-producing countries are probably present there in small numbers and in different proportions. For example, a large proportion of salmon originating from the United States and a small proportion of Norwegian fish are present in this area. In the Norwegian Sea, fish from Norway are most abundant, but there are relatively high proportions of fish from the UK (Scotland) and Russia in this area, and smaller proportions from other areas of Europe. Fish of North American origin have also been observed there. Atlantic salmon home with high precision to the rivers they left as smolts. The homing migration seems to consist of two phases: a first phase with crude navigation from oceanic waters to coastal areas, and a second phase with more precise navigation in coastal and estuarine waters towards the home river. The underlying mechanisms explaining these migrations are still a matter of controversy, but apparently the juvenile fish learn their way (imprint) sequentially and use that information to return home. During the oceanic phase, salmon are thought to use celestial cues, magnetic fields, or a combination of different cues. The olfactory sense plays a major role for the final orientation in fjords, estuaries, and rivers.

Keywords: farmed salmon, marine distribution, migration, tagging, wild salmon.

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Introduction

Atlantic salmon (*Salmo salar* L.) undertake long migrations on their way from freshwater to the feeding areas in the ocean and on their return to freshwater. There is substantial information on Atlantic salmon in freshwater, but in contrast, much less is known about the sea life (e.g., Hansen and Quinn, 1998; Jacobsen, 2000). The main reason for this is the easy access to sampling salmon in freshwater as opposed to marine sampling.

When coastal fisheries developed more than 100 years ago, some information became available on salmon in the local environment, but the distribution and migration of salmon in oceanic areas was a "black box" until oceanic fisheries developed in the 1960s at West Greenland and in the northern Norwegian Sea. To assess these fisheries and provide more information from oceanic areas, ICES took initiatives to organize joint international investigations to study the problem (Parrish and Horsted, 1980, and a large number of ICES working group reports). This was a major breakthrough in salmon research in the ocean. However, these investigations did not address the distribution of fish outside the fishing seasons and areas.

The mortality of salmon in the sea was suggested as taking place during the first months after the smolts left freshwater, but little was known about this life stage (e.g., Doubleday *et al.*, 1979; Ritter, 1989). Research on this issue was strongly recommended by ICES, but only recently have systematic efforts been made to sample postsmolts at sea (Reddin and Short, 1991; Holst *et al.*, 1993; Shelton *et al.*, 1997; Holm *et al.*, 2000). This, together with knowledge gained from an oceanic research programme on salmon at the Faroe Islands, also recommended by ICES (Jacobsen, 2000), has improved

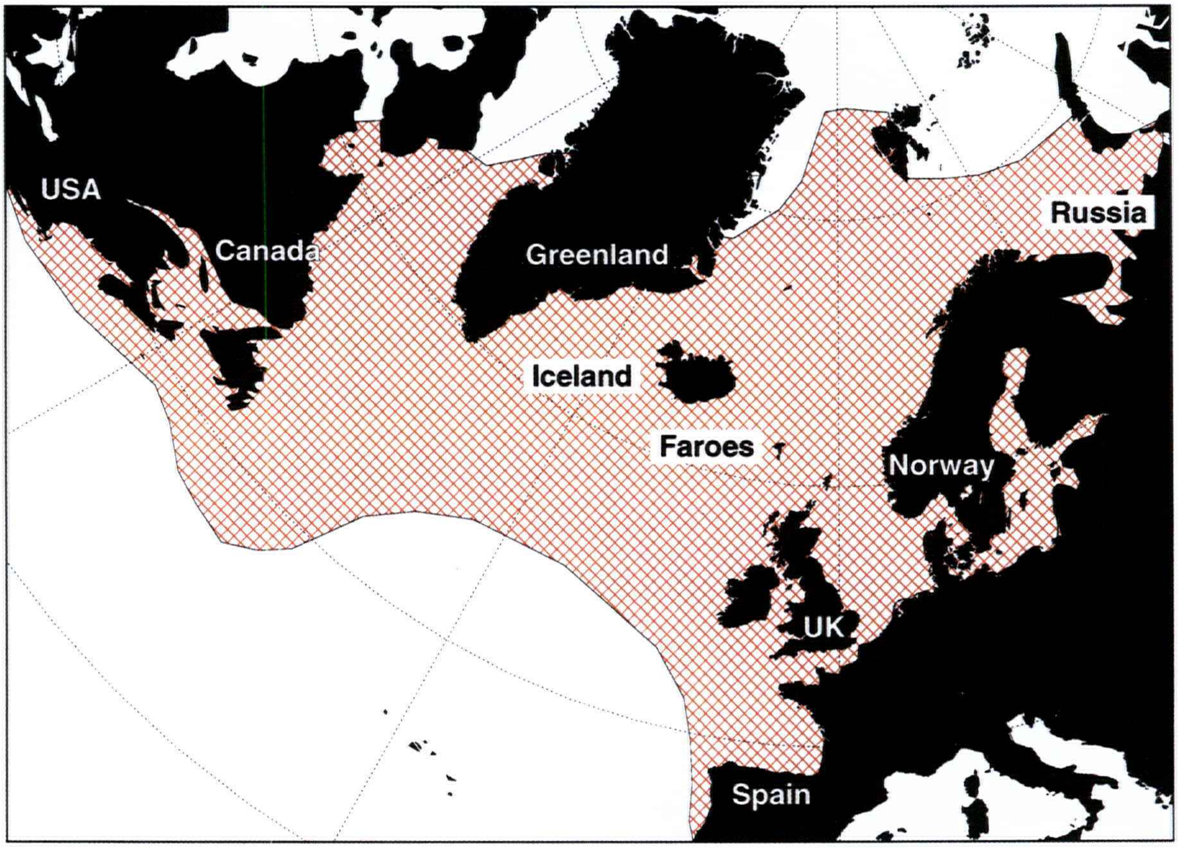

Figure 1. Approximate oceanic distribution of Atlantic salmon in the North Atlantic.

our understanding of salmon biology in the ocean, but there are still major gaps.

The aim of this paper is to review some aspects of the life history of Atlantic salmon, particularly the marine distribution and migration of the fish, and to discuss possible mechanisms explaining homing migration of the species.

Life history of Atlantic salmon

Atlantic salmon are well known for their anadromous life history. Adults spawn in freshwater in the autumn, the embryos incubate in gravel stream beds over the winter, and emerge in spring as fry. Depending on conditions, they spend 1–7 years in freshwater as parr before undergoing a transformation into seaward-migrating smolts. The post-smolts undertake a long journey in the ocean, and as maturing adults, salmon return with high precision to their natal rivers to spawn. Although anadromy is the most common life history pattern, resident individuals and populations of the species are well known, as in other salmonids (Jonsson and Jonsson, 1993). Sexually mature male parr are common in many populations, and some may smolt the following spring and go to sea (e.g., Mills, 1989).

Atlantic salmon are probably adapted to the prevailing environmental conditions that they encounter both in freshwater and at sea. The result of these adaptations is that, despite overlapping marine distributions, salmon spawned in different rivers vary in life history traits such as growth rate, age at sexual maturity, migration pattern and seasonal timing of return, frequency of mature male parr, resistance against diseases and parasites, survival rate in freshwater and at sea, and time of spawning (e.g., Saunders, 1981; Heggberget, 1988; Bakke *et al.*, 1990; Hansen and Jonsson, 1991; Hindar *et al.*, 1991; Taylor, 1991). The homing of adults to their natal streams and the different regimes of natural selection in the streams explain why Atlantic salmon are subdivided into discrete genetic populations localized to specific rivers, tributaries, or parts of rivers (e.g., Ståhl, 1987; Hindar *et al.*, 1991).

Atlantic salmon are distributed over large areas in the North Atlantic during their migrations between freshwater and their feeding grounds at sea (Figure 1). They can

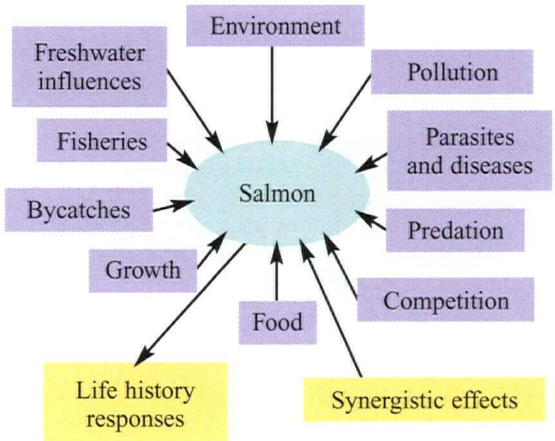

Figure 2. Important factors affecting salmon at sea.

be found from Connecticut to Ungava Bay in eastern North America, and in Europe from northern Portugal to the border between Europe and Asia in northern Russia. Atlantic salmon are also present around the British Isles, Ireland, Iceland, and Greenland. In some oceanic areas (e.g., the Norwegian Sea, north of the Faroe Islands, and between West Greenland and Labrador), the number of immature salmon has been sufficient to encourage commercial fisheries. The brackish waters of the Baltic Sea also support a form of Atlantic salmon (called Baltic salmon) that only rarely moves into the Atlantic Ocean, but rather feeds in the southern Baltic Sea. Atlantic salmon may spend 1–5 years in the ocean until they become sexually mature and return to the home rivers to spawn. Depending on the population and the duration of marine residence, they may range from 1 to 30 kg in weight.

Survival from smolt to adult varies considerably among stocks and years, but is highest for salmon that have spent one winter at sea (known as grilse or one-sea-winter (1SW) fish). Many factors affect the marine survival of Atlantic salmon (Ritter, 1989), although they are generally poorly understood (Friedland and Reddin, 1993; Reddin and Friedland, 1993). Some of these factors are outlined in Figure 2. The parr–smolt transformation (smolting) and the post-smolt stage (the period just after the smolts have left the rivers) are of particular interest because these periods may be critical for survival in the sea (e.g., McCormick *et al.*, 1998). Friedland *et al.* (2000) showed that post-smolt growth was enhanced in years with favourable temperature conditions, which in turn resulted in higher survival rates.

Atlantic salmon spawn in the autumn, and in contrast to Pacific salmon, many fish may survive spawning, return to the ocean, and return home a second time to spawn. Post-spawning mortality is higher in males than in females and higher in large than in small fish (Jonsson *et al.*, 1997).

Marine distribution of Atlantic salmon

In Atlantic salmon, there is evidence that the marine distribution of this species is dependent on temperature (Reddin and Shearer, 1987), but whether the distribution of food is an important factor is still an open question. The reason for this is the fact that the biomass of Atlantic salmon in the ocean relative to other pelagic oceanic fish species is extremely small.

Atlantic salmon smolts leave freshwater, and the post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g., Thorpe, 1988; Mills, 1989). When moving down rivers and entering marine waters, their movements seem to depend on the speed and direction of surface currents (McCleave, 1978; LaBar *et al.*, 1978; Holm *et al.*, 1982; Jonsson *et al.*, 1993). Most of the records available suggest that post-smolts move relatively quickly into the ocean, swimming as fast as two body lengths s^{-1} (Lacroix and McCurdy, 1996), after a period of more passive movements with tidal currents. The duration of estuarine residence seems to be relatively brief. Further evidence, albeit indirect, of rapid migration comes from the fact that very few post-smolts are recorded in fjords and coastal waters during summer and autumn, although they are already present in oceanic areas in the East Atlantic (Holm *et al.*, 2000; Holst *et al.*, 2000) and West Atlantic (Reddin and Short, 1991) at this time of year. However, Dutil and Coutu (1988) caught many post-smolts in a near-shore zone of the northern Gulf of St. Lawrence, suggesting that this trait may vary among populations or areas. Friedland *et al.* (1998) also found evidence that post-smolts in some years used the Gulf of St. Lawrence as a nursery area prior to seaward migrations.

A number of post-smolts have been caught in oceanic areas of the Northeast Atlantic in recent years during pelagic trawl surveys in the Norwegian Sea in July and August (Holm *et al.*, 2000) and north of Scotland in May and June (Holm *et al.*, 1996; Holst *et al.*, 1996; Shelton *et al.*, 1997). Based on the distribution of catches north of Scotland, the fish appeared to move northwards with the shelf edge current (Shelton *et al.*, 1997). Farther north in the Norwegian Sea, post-smolts were caught beyond 70°N in July. Analysis of growth and smolt age distribution strongly suggested that most of the post-smolts originated from rivers in southern Europe (Holst *et al.*, 1996). This was supported by the recapture of a salmon that had been tagged in April 1995 in southern England and recovered about 2000 km farther north three months later, demonstrating the capacity for rapid travel by post-smolts (Holst *et al.*, 1996).

In the Labrador Sea, Reddin and Short (1991) caught many post-smolts in the early autumn of 1987 and 1988 using surface drift nets. The highest catch rates occurred between 56 and 58°N, and they also caught many older salmon in the area. Based on age analysis, they concluded that post-smolts originating from Maine to Labrador were present. This was supported by recoveries of two post-smolts that had been tagged in the Penobscot River in Maine and Western Arm Brook, Newfoundland. In addition, four older fish in the Labrador Sea had tags, three from the Penobscot River and one from the Middle River, Nova Scotia.

When Atlantic salmon have reached catchable size, their marine distribution is easier to document. Many countries have had major tagging programmes on smolts and adults, and some of these fish have been recaptured in the high-seas fisheries. It is difficult to know the true distribution of salmon at sea, as recoveries depend on the distribution of fishing effort. However, the absence of fishing pressure in an area does not demonstrate the absence of salmon, although one may assume that there is at least some general correspondence between the distributions of fish and fishermen. The waters off the west coast of Greenland contain many immature salmon that have spent one winter at sea (1SW) or more than one winter at sea (multi-sea winter or MSW fish). Here, fish from both North America and Europe feed during June–September and are exploited.

The concern generated within the main Atlantic salmon-producing countries in the North Atlantic following the rapid growth of the West Greenland salmon fishery in the early 1960s, and the great scientific interest in gaining more knowledge of salmon during the marine phase, led to steps taken by the International Commission for the Northwest Atlantic Fisheries (ICNAF) and ICES at their annual meetings in 1965 to establish a scientific Working Party on North Atlantic Salmon. The Working Party's most important tasks were to coordinate data collection and research programmes. In 1980, ICES published a comprehensive report from these joint investigations (Parrish and Horsted, 1980). Results from these investigations encouraged scientists to develop improved methods for assessments and estimation of stock distribution of salmon in this area, as well as stimulating research on salmon to be initiated at sea also in other areas of the North Atlantic.

In summary, Swain (1980) analysed a time-series of smolt taggings in European rivers in relation to recaptures off West Greenland, as did Ruggles and Ritter (1980) for North American smolt taggings. Møller Jensen (1980a) used tag recoveries from West Greenland in 1972 to assess the distribution along the West Greenland coast of salmon originating from North America and Europe. These investigations showed that Atlantic salmon from a number of different rivers in North America and Europe were present in the area. Furthermore, based on much more comprehensive material, Reddin (1988) and Reddin *et al.* (1988) used discriminant analysis of scale characteristics and concluded that catches of salmon off West Greenland were split fairly evenly between the two continents. It is more difficult to determine the country of origin, but Canada accounts for most of the North American component and Scotland for most of the European fish (Møller Jensen, 1980a). However, in recent years, the proportion of salmon originating from Europe seems to have decreased (Reddin and Friedland, 1999). All in all, salmon tagged as smolts in home waters and recaptured at West Greenland have originated from Canada, the United States, Scotland, England, France, Norway, Sweden, Iceland, and Ireland, and some Russian salmon may also be present in the area.

At the end of the 1960s and beginning of 1970s, the ICES/ICNAF joint tagging experiments took place off West Greenland (Møller Jensen, 1980b). A total of 4657 salmon were tagged and 93 fish were recaptured outside Greenland: 28 in North America and 65 in Europe. The tags were reported from the United Kingdom (44), Canada (28), Ireland (16), Spain (3), and France (2). Taking into account the production of smolts in these countries, this suggests that larger proportions of salmon from more southern areas of Europe are present in this area than from farther north.

In the East Atlantic, salmon are found in large areas in the Norwegian Sea. In the 1970s, there was an important commercial longline fishery far north in the Norwegian Sea in February–May. The concern of the effects on salmon stocks caused by this fishery resulted in recom-

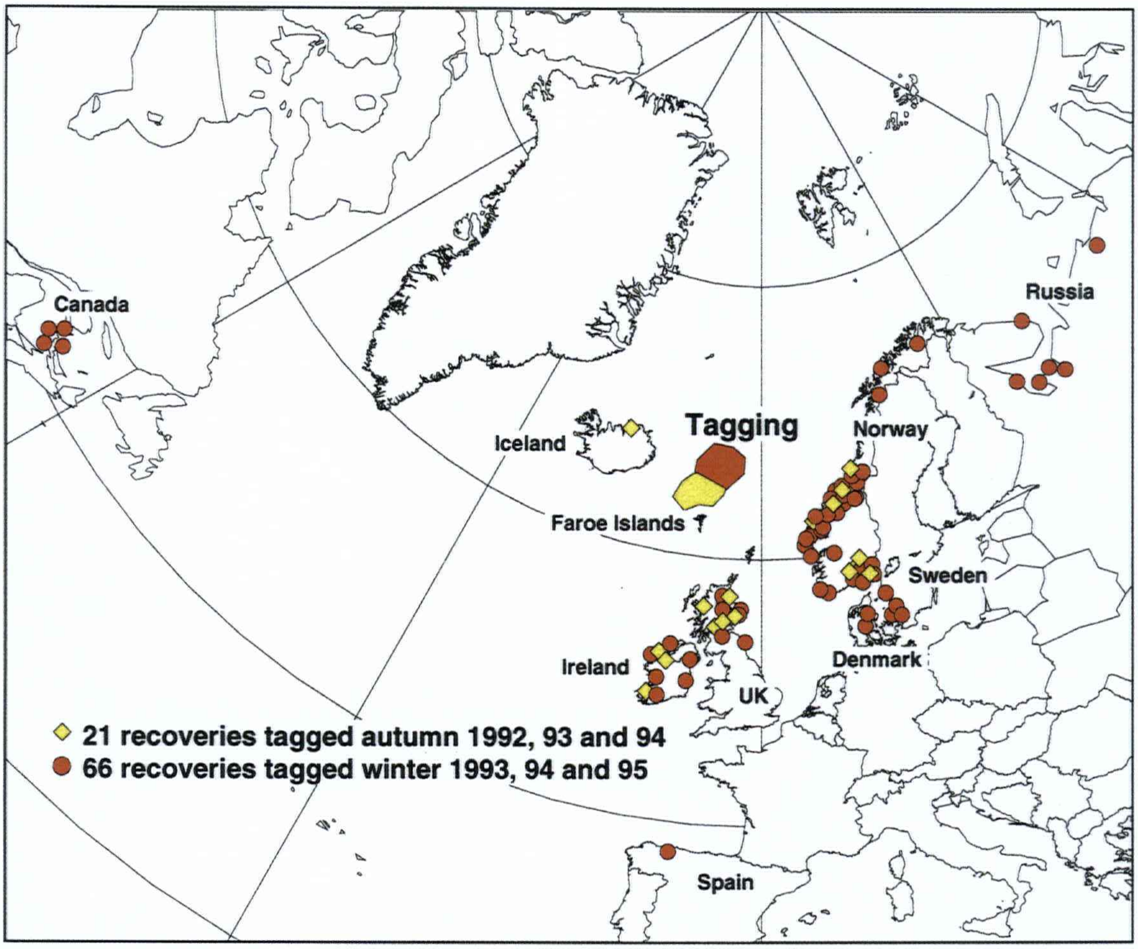

Figure 3. Recoveries of wild Atlantic salmon tagged during the 1992/1993–1994/1995 fishing seasons. Fish were tagged north of the Faroes during autumn (November/December: yellow shading) and winter (February/March: red shading). Recoveries from each tagging period are shown as yellow diamonds (autumn tagging) and red circles (winter tagging). From Hansen and Jacobsen (2000).

mendations from ICES to collect information on stock composition as well as to estimate effects on home-water stocks. Recoveries of fish in this fishery that had been tagged as smolts, and recaptures in coastal and freshwater fisheries of salmon tagged in the Norwegian Sea, suggested that Norwegian salmon were most abundant, although fish from the United Kingdom, Sweden, and Russia were also present. Most of the fish were recaptured in home waters the same year they were tagged, suggesting that they were maturing (Rosseland, 1971). Towards the end of the 1970s, fishing for salmon in the northern Norwegian Sea was banned, and fishing was limited to the area within the Faroese Exclusive Economic Zone (EEZ).

The abundance of salmon within the Faroese EEZ has been assessed from sampling the fishery for a number of years. Jákupsstovu (1988) reported on a tagging programme at sea from 1969 to 1976 in which 1946 salmon caught on longlines were tagged and released. The fish were tagged in more southerly areas of the Faroes, and 1SW fish were probably highly overrepresented. In total, 90 fish were recovered: 33 in Scotland, 31 in Norway, 15 in Ireland, 8 in other European countries, and 3 at West Greenland. The great majority of the tags were reported in home waters the same year they were tagged. However, it is interesting to note that some fish in the area may have been on their way west, as they were reported from West Greenland later that year.

In recent years, a tagging programme has been carried out in the major fishing grounds north of the Faroes. The project was initiated as a bilateral effort between the Faroes and Norway, with financial support also from the Nordic Council, and endorsed by ICES. From November to March in the 1992/1993, 1993/1994, and 1994/

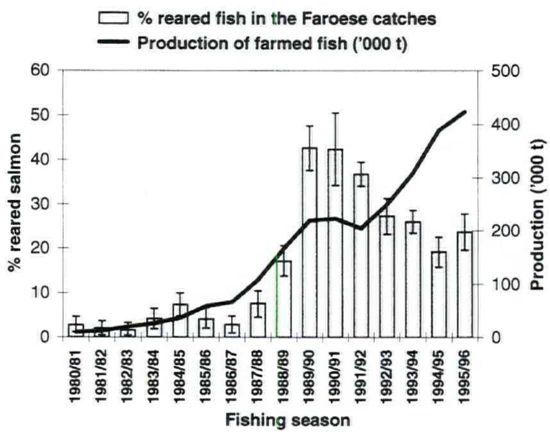

Figure 4. Production of farmed salmon in the Northeast Atlantic and estimated percentage of escaped farmed salmon caught in the Faroese longline fishery for salmon. Error bounds (95% confidence limits) on the separation of catch into wild and farmed salmon are indicated (Monte Carlo simulation, 2000 simulations using @Risk). From Hansen *et al.* (1999).

1995 fishing seasons, 5456 salmon (3811 wild and 1637 farmed) were caught by longline, tagged, and released (Hansen and Jacobsen, 2000). In total, 106 fish (87 wild and 19 farmed) have been recaptured. Wild salmon of Norwegian origin were most abundant in the area, but Scottish and Russian salmon were also common. Some additional recaptures were reported from Ireland, Iceland, Spain, Sweden, Denmark, England, and even Canada (Table 1; Hansen and Jacobsen, 2000). Detailed geographical distribution of the recoveries is given in Figure 3 (Hansen and Jacobsen, 2000). Of the escaped farmed salmon, 18 were recaptured in Norway and one at the west coast of Sweden.

The distribution of Atlantic salmon in the ocean is still not well known, but the limited information indicates that salmon are not evenly distributed. Salmon from North America seem to stay in the West Atlantic area, although some fish can move into the Northeast Atlantic. It is also evident that a relatively large proportion of the European MSW salmon moves far into the West Atlantic to feed. Salmon from many populations differ in how long they stay at sea, hence different sea-age classes from the same populations may be present in different areas (Jacobsen *et al.*, 2001). For example, MSW salmon may move farther away from home than grilse, as suggested by Scarnecchia (1989) for salmon originating in Iceland. A better map of Atlantic salmon distributions at sea in time and space would help us to understand the fluctuations in their survival and life history. The distribution of Atlantic salmon in the sea seems to reflect environmental factors like surface temperature and surface currents (Reddin and Friedland, 1993), and probably also the availability of suitable food organisms (Jacobsen and Hansen, 2000), as growth and survival are important fitness characters as well.

In addition to the wild Atlantic salmon, there has been a great increase in the abundance of reared fish in recent years. In Iceland, major sea ranching programmes have been carried out (Isaksson, 1988). In several countries, especially Norway and Scotland, a huge salmon farming industry has also developed. Escaped farm fish have been observed in several areas in the Northeast Atlantic, and they contribute substantially to salmon fisheries in Norway and the Faroes. In Norway, recent estimates suggested that nearly 50% of the salmon catch in coastal bagnets was escaped farmed fish (Lund *et al.*, 1996), and at the Faroes in the fishing seasons 1989–1992, more than 40% of the catch was estimated to be of farmed origin. Later, this proportion has declined to about 25%, probably as a result of improved security of the farms (Figure 4; Hansen *et al.*, 1999). At West Greenland, the incidence of farmed fish appeared to be very small (Hansen *et al.*, 1997). In 1997, ICES and the North Atlantic Salmon Conservation Organization (NASCO) held an international symposium on "Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues". Pro-ceedings and reports can be found in Hutchinson (1997) and Youngson *et al.* (1998).

Migration of salmon

Oceanic homing migration

Atlantic salmon leave the oceanic feeding grounds after 1–4 years. The factors initiating the homeward migration are unknown, but salmon have circannual rhythms of reproductive hormones, synchronized by photoperiod (Bromage *et al.*, 1993). The usual pattern is that the older individuals return earlier in the season than do younger ones (e.g., Dunkley, 1986; Jonsson *et al.*, 1990; Shearer, 1992). The internal rhythms and responses to photoperiod may be population-specific. For example, salmon ascend several Scottish rivers during all months of the year (e.g., Mills, 1989), whereas in Norway, salmon ascend rivers only from May to October. There is direct evidence for a genetic component in the seasonal return migration of Atlantic salmon (Hansen and Jonsson, 1991).

The mechanisms underlying salmon orientation in the ocean are still a matter of controversy, and most of the information is reported from the Pacific. From extensive data on tagged Atlantic salmon, Hansen *et al.* (1993) concluded that the homing migration from the feeding areas in the northern Norwegian Sea to natal rivers in Norway consists of two phases: an initial phase with orientation from the feeding areas towards the Norwegian coast and a second phase in coastal and estuarine waters with more precise orientation towards the

Table 1. Recaptures in number of wild salmon in different countries tagged at the Faroes during the 1992/1993, 1993/1994, and 1994/1995 fishing seasons. From Hansen and Jacobsen (2000).

Country	Tagged 1992/1993		Tagged 1993/1994		Tagged 1994/1995		Total	
	Rec. 93	Rec. 94	Rec. 94	Rec. 95	Rec. 95	Rec. 96	No.	%
Norway	22	3	2	–	17	3	47	54
Scotland	8	–	1	–	3	–	12	13.8
Ireland	3	–	2	–	4	–	9	10.3
Sweden	2	1	–	–	1	–	4	4.6
Russia	1	1	3	–	1	–	6	6.9
Canada	1	–	–	–	3	–	4	4.6
Denmark	2	–	–	–	–	–	2	2.3
England	1	–	–	–	–	–	1	1.1
Iceland	1	–	–	–	–	–	1	1.1
Spain	1	–	–	–	–	–	1	1.1
Total	42	5	8	0	29	3	87	99.8

home river. Hansen *et al.* (1993) estimated that salmon travelled 50–100 km/d in the Norwegian coastal current.

Behavioural experiments with juvenile Pacific salmon indicate that they are sensitive to the magnetic field of the earth (Quinn, 1980; Quinn and Brannon, 1982) and magnetite particles may be a component of the transduction mechanisms (Walker *et al.*, 1988; Moore *et al.*, 1990). Such a magnetic-field detection system could aid in navigation, but no conclusive experiments have been conducted on this subject.

Alternatively, the salmon may possess a compass orientation ability and head in a homeward direction without regard to their location at sea. This hypothesis is consistent with experimental evidence that juvenile salmon can orient using the sun's position (Groot, 1965) and magnetic field (Quinn, 1980; Quinn and Brannon, 1982). The ability of telemetered Atlantic and Pacific salmon to swim in relatively straight lines in open water indicates at least some directional ability (Smith *et al.*, 1980; Quinn *et al.*, 1989; Ogura and Ishida, 1995), and rapid rates of net travel could not be accomplished without a good sense of direction, given the swimming speeds of salmon (Quinn and Groot, 1984).

In addition to the map and compass hypotheses, it is possible that salmon migration at sea is guided by information emanating from freshwater locations. However, the distances that salmon travel from their home river, the complex current patterns at sea, and the tendency of salmon to return home from different feeding locations makes it very unlikely that riverine odours play an important role in the open ocean (Royce *et al.*, 1968), and it is generally accepted that the stimuli guiding salmon at sea differ from those used in rivers (Hasler, 1971; Quinn, 1990).

Coastal homing migration

After salmon accomplish the migration from distant, oceanic, feeding grounds to the nearshore environment, the coastal waters and estuaries present another set of challenges to their orientation systems. The homing migration of Atlantic salmon does not seem to be passive or current-progressed, as suggested by Taguchi (1957), Mathisen and Gudjonsson (1978), and Isaksson (1980). When homing to Norwegian rivers, the fish approached the fjords from both the north and south and may have followed the coastline for long distances (Hansen *et al.*, 1993). A similar pattern has also been observed along the east coast of Canada (Reddin and Lear, 1990). Salmon tracked by Smith *et al.* (1980) off the east coast of Scotland showed the ability to swim in fixed directions at energetically efficient speeds, but they were also affected by tidal currents.

Hansen *et al.* (1993) reported that Atlantic salmon travel rates slowed in fjords, perhaps because they required time to locate their natal rivers. Westerberg (1982a) and Døving *et al.* (1985) reported that telemetered salmon moved up and down in the water column in association with fine-scale hydrographic stratification, and they concluded that salmon search for vertical gradients of odours from the home river rather than horizontal gradients.

Alternatively, the apparently random movements of many salmon in coastal waters and estuaries may not reflect orientation mechanisms, but rather the tendency of many populations to wait for suitable conditions for upstream migration (Jonsson *et al.*, 1990) or to remain in the estuary as they undergo the physiological processes of maturation and osmoregulatory adaptation to freshwater. Atlantic salmon tracked in estuaries of the Baltic Sea (Westerberg, 1982b), Nova Scotia (Brawn, 1982), and England (Potter, 1988; Priede *et al.*, 1988) tended to move back and forth with tidal currents for some time before ascending their home rivers.

Homing mechanisms

Although olfaction probably plays a minimal role in the orientation of salmon in the open ocean, it is well established that odours guide the final stages of homing in freshwater. A large body of evidence indicates that odours inherent in the stream (e.g., rocks, soil, plants) provide a distinctive chemical signature that is learned ("imprinted") by juvenile salmon prior to or during seaward migration and is used by maturing adults to identify their natal streams (Hasler, 1966; Harden Jones, 1968; Hansen *et al.*, 1989). It has also been hypothesized that population-specific odours (pheromones) from conspecifics living in the river or migrating to sea, guide maturing salmon (Nordeng, 1977). Most evidence supports the first hypothesis. Atlantic salmon released as smolts in a small stream devoid of salmon returned there to spawn at maturity (Hansen *et al.*, 1989). Pacific salmon also returned to their release site rather than to a site containing members of their population (e.g., Donaldson and Allen, 1957; Brannon and Quinn, 1990) and can home to rivers scented with artificial odours which they imprinted, even in the absence of pheromones (Hasler and Scholz, 1983).

Experimental transportation and release studies indicate that salmon may not merely imprint once in freshwater, but rather that cues are learned in a more complex sequence. Atlantic salmon released as smolts in the River Imsa returned there as adults with high precision (Hansen *et al.*, 1989). However, when smolts imprinted to River Imsa water were transported by boat about 45 km towards the ocean, and were thus deprived of a part of the migration route, the great majority of the adults failed to return to the River Imsa, suggesting that the salmon needed to experience the outward migration in order to find their home river at maturity. Atlantic salmon transported and released as post-smolts on the feeding grounds north of the Faroe Islands failed to home as adults to their home river; in fact, no fish was reported caught in freshwater (Hansen *et al.*, 1993). This may indicate a reduced preference for these fish to enter rivers and spawn. All adult recaptures, however, were made in Norwegian home waters eastward of the site of release. No maturing salmon were reported from elsewhere despite heavy salmon fishing in the United Kingdom, Ireland, and North America, and in Icelandic rivers. Natural mortality of post-smolts in the sea is high (e.g., Mills, 1989), and the recaptures are few and scattered over large areas. However, the fact that all adult recaptures of the released post-smolts were reported from Norwegian home waters supports the idea that salmon may have an inherited crude compass for sensing of direction (Walker *et al.*, 1988; Moore *et al.*, 1990), and that sequential learning may not be mandatory to sense the general direction back to home waters.

Hansen and Jonsson (1994) provided evidence to support the hypothesis that the learning process during smolt migration to the sea becomes fixed and is not overridden by a new learning process at the post-spawning stage. Kelts transplanted from their home river to several distant rivers returned as second-time spawners to the river they left as smolts, not to the river from which they entered the ocean as adults.

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