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**Report describing a conceptual migration and
ecological model**

(Month 40)

Introduction

The SALSEA-Merge objectives addressed by the issues considered in this report relate to the development of a conceptual migration and ecological model for young salmon the first months at sea. Presented here is a summary of the activities and outcomes relating to the integration of oceanographic information, surface currents, etc., from an ocean model, with biological information and observed genetically determined population distribution and origins, to construct an integrated conceptual ecological and migration model of post-smolt migration and distribution. This report arises from the work carried under WP5 Task 5.2 Development of a conceptual migration and ecological model for young salmon at sea. The report is in two parts. The first part addresses the modeling of the migration pattern of young salmon for different European stocks. The second part of the report describes the different factors related to the distribution, mortality and growth of young salmon in the ocean that is put together in a conceptual ecological model.

Background

The migration patterns of post-smolt salmon still remain largely unknown. In order to understand ocean migration behaviour of salmon and make predictions of their survival, it is necessary to obtain a more complete picture of how Atlantic salmon are dispersed in the sea in time and space. Atlantic post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g. Thorpe, 1988; Mills, 1989). After the post-smolts enter the ocean, their migration pattern is little known, due to the relatively small number of fish captured relative to the potential migration area. It has been hypothesised that the major post-smolt mortality occurs in the first weeks or months after the smolts have left freshwater. The distribution, mortality and growth of salmon in the ocean are related to sea surface temperature (e.g. Reddin and Shearer, 1987) although other factors are known to be important. The advance in ecological models of salmon has been hampered by the lack of knowledge on behavioural processes that determine migration and distribution of salmon.

To address this, a conceptual migration and ecological model are developed by using oceanographic fields (such as ocean currents) from the three-dimensional Regional Ocean Modelling System (ROMS) ocean model, together with the post-smolt distribution data acquired in previous WPs. Several different biological and oceanographic associations/hypothesis on swimming behaviour identified in the previous subtasks are tested using a particle tracking model, which will be based on the velocity fields identified from the ocean model.

The migration model

Introduction

Atlantic salmon smolts leave fresh water and the post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g. Thorpe 1988; Mills 1989). The duration of estuarine residence seems to be relatively brief (Thorstad et al 2007). 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). When they have reached oceanic areas they distribute over large areas of the North Atlantic (Holm et al. 2004). In the marine phase, they feed in surface waters, and mainly occupy the upper 30 m of the water column, but with some occasional dives to larger depths (Holm et al. 2004). At the population level, the distribution at sea is not known, but fish originating from several rivers have been shown to be present in the same areas (Hansen and Jacobsen 2000; Hansen and Jacobsen 2003). The distribution at sea probably depends on a combination of factors such as food availability, water temperature and currents, as well as on genetic components that govern population specific navigation systems (Hansen and Quinn 1998; Holm et al. 2004).

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). For migratory fishes, such as Atlantic salmon, temporal variation in the utilization of thermal and depth habitats in the marine environment is likely to occur at both broad and fine scales, reflecting ecological and metabolic factors (Hansen and Quinn, 1998; Jonsson *et al.*, 2003; Friedland *et al.*, 2003).

As post-smolts, their distributions continue to be regulated by passive transport mechanisms and limited by swimming ability (Friedland et al. 1999; Holm et al. 2000). During this time, post-smolts are exposed to the prevailing climatic conditions and it is not until some point later in the post-smolt year that the swimming ability of the salmon begins to exceed current velocities and they are able to actively pursue a preferential habitat (Friedland et al. 1999).

The alteration of suitable migratory pathways has been suggested as a factor in the survival of North American post-smolts (Friedland et al. 1999) and should be considered for European stocks, as well. Migratory species are known to change routes in association with changing currents, temperature and salinity distributions (Minns et al. 1995; Ottersen et al. 2004), and habitat shifts in response to climatic alterations have already been reported for many species in the North Sea (Perry et al. 2005). The nursery habitat for Atlantic salmon is dynamic and depends integrally on the abundance of primary production to support a prey base. If post-smolts are forced to swim greater distances in order to discover suitable thermal habitat, a growth effect may be detected.

The migration patterns of post-smolt salmon still remain largely unknown. In order to understand ocean migration behaviour of salmon and make predictions of their survival, it is necessary to obtain a more complete picture of how Atlantic salmon are dispersed in the sea in time and space. Atlantic

post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g. Thorpe, 1988; Mills, 1989).

Model description

To investigate and increase our understanding of salmon migration we have used a 3D hydrodynamical model (ROMS – Haidvogel *et al.*, 2008 - www.myroms.org). Monthly mean lateral boundary conditions were taken from a global version of ROMS with a resolution of about 20 km in the North Atlantic and Arctic, and comprise of 3D velocities, sea surface height (SSH), temperature and salinity. In addition, 8 tidal constituents from the Oregon State University TOPEX/Poseidon Global Inverse Solution (TPXO 7.0; Egbert *et al.*, 1994; Egbert and Erofeeva, 2002) were added to the SSH and barotropic flow at the lateral boundaries. Six-hourly vertical boundary conditions were taken from ERA40 interim (www.ecmwf.int) and included sea surface air pressure, wind stress, latent, sensible, downward shortwave radiative and net longwave radiative heat flux. The model domain covers the North-East Atlantic, Nordic seas, North Sea, Barents Sea, Kara Sea, and partly the Arctic (Figure 1) and has a spatial resolution of 4 km, with 30 s-coordinates (stretched, terrain-following) in the vertical. Daily averages were stored on disk for use in an offline particle-tracking model (Ådlandsvik and Sundby, 1994) for transport of particles from the release locations.

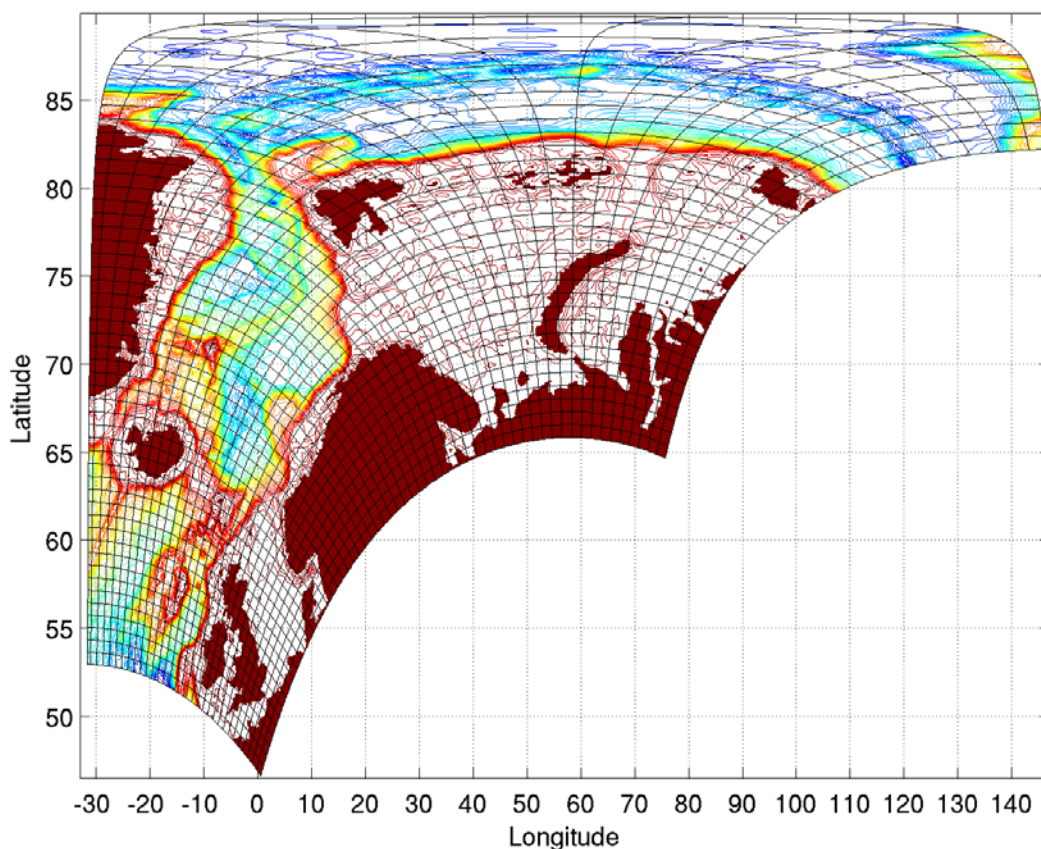


Figure 1. The model domain. The horizontal resolution is 4 km.

Consistent with recommendations by ICES (2009), the particle-tracking algorithm use daily mean velocity and temperature fields from the ocean model (GCM), which is state-of-the-art, including a 4th-order Runge Kutta advection scheme and bilinear 3D interpolation of daily mean velocity and temperature fields. Tides are part of the ocean simulation but these are averaged out when stored on disk.

The ocean model has been used and evaluated in several other works (e.g. Vikebø et al., 2010). In Vikebø et al. (2010), the simulation reproduced the hydrographic and circulation features in the Svinøy section, a section in the southern Norwegian Sea (0°E, 65°N to 5°E 62.3°N) for long-term monitoring of the hydrographic and ocean current conditions. The modelled annual mean volume flux of the Norwegian Atlantic Slope Current for 1997-1999 was identical to the values obtained by Orvik *et al.* (2001) for the same period (4.2 Sv). The strong seasonal signal in the volume transport with a maximum in winter was agreement with the observations. An example of modelled ocean current is shown in Figure 2. Warm waters from the North Atlantic flow into the Norwegian Sea, mainly through the Faroe-Shetland Channel, and northwards. Cold Arctic waters flow southwards along the East coast of Greenland and parts of it flow into the Iceland Sea, as the East Icelandic Current, and into the Norwegian Sea. These two main currents make the hydrographic conditions in the Nordic Seas: warm water in the east, and cold water in the west.

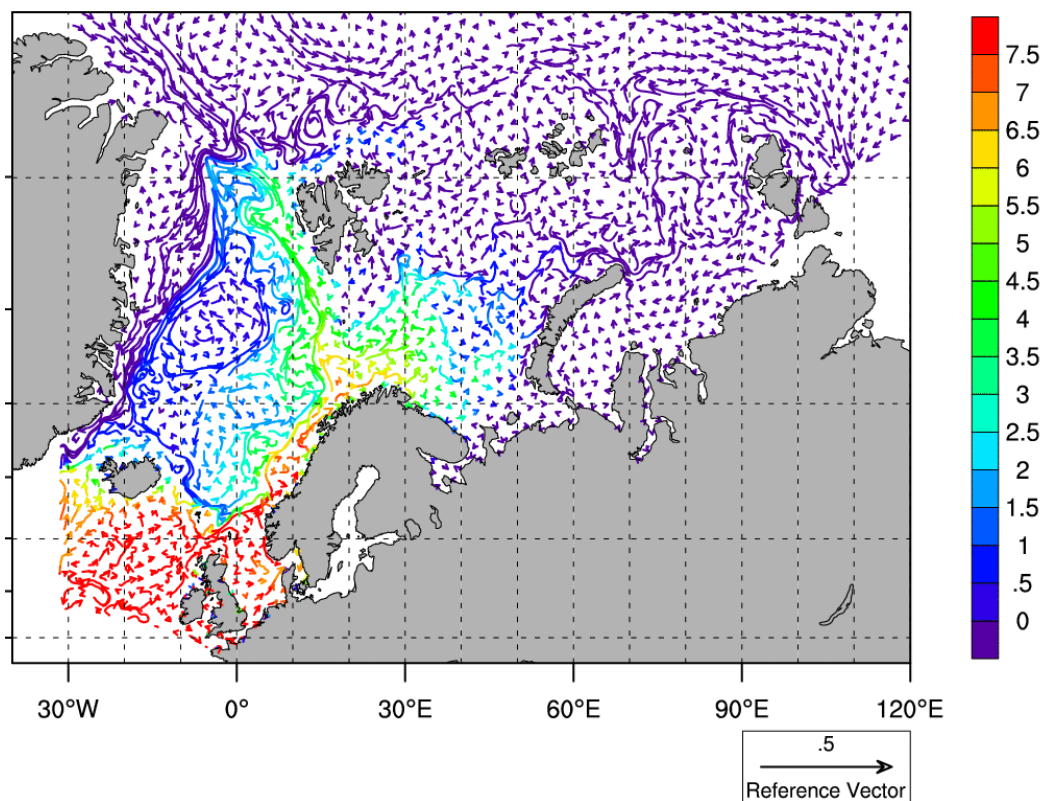


Figure 2. Modeled ocean current at 50 m depth in February 2007. Colors indicate water temperature.

Active migration speed

The distribution at sea probably depends on a combination of factors such as food availability, water temperature and currents, as well as on genetic components that govern population specific navigation systems (Hansen and Quinn 1998; Holm et al. 2004). A number of post-smolts have been caught in oceanic areas from the North Sea to the Norwegian Sea during pelagic trawl surveys in the Norwegian Sea in July and August (Shelton et al. 1997; Holm et al. 2000; Holm et al. 2004), and north of Scotland in May and June (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). Earlier surface trawl surveys in the Norwegian Sea have revealed a close association between post-smolt captures and the warm saline water typical of the North Atlantic Current, as almost all captures have been made in water salinities above 35 and temperatures between 8-11 °C (Holm *et al.* 2004; Holm, Holst & Hansen 2000).

91 tagged smolts, recaptured from 1996 to 2009, are used to estimate the active swimming speed of the post smolts. These fishes originate mainly from Ireland, but few fish also from Norway (Figure 3).

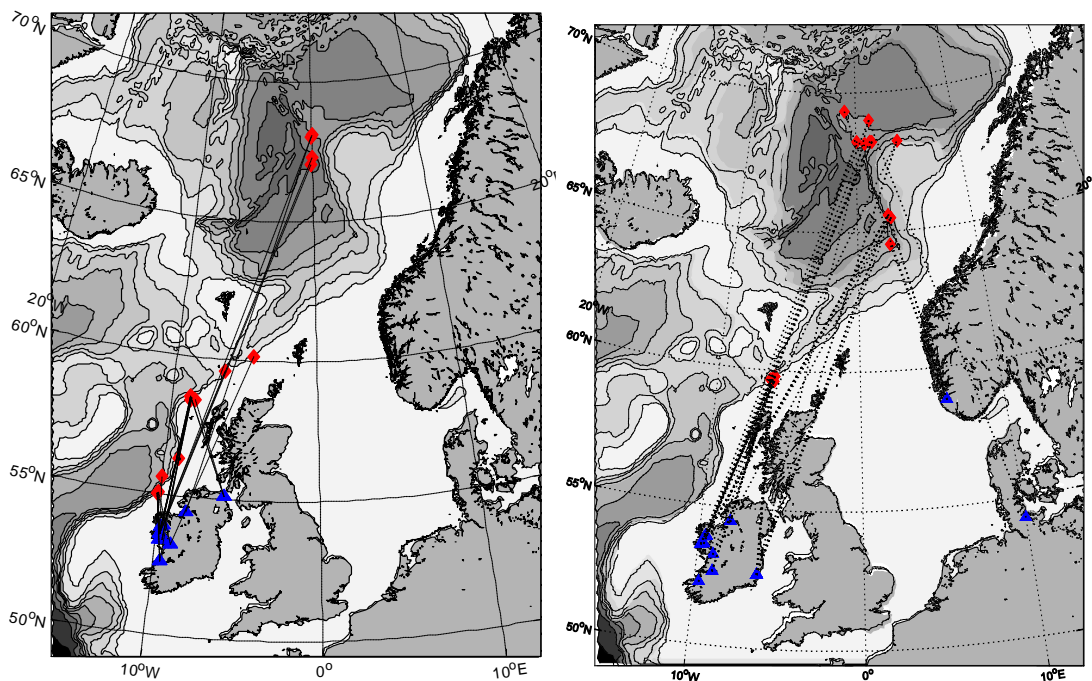


Figure 3. Recaptured tagged fish. Left figure: 33 tagged post smolts (2008-2009). Right figure: 58 tagged post smolts (1996-2003).

The migration speed of post smolts is a sum of drift with the ocean currents and active swimming. Based on captured post smolts (distribution) we define a likely migration path for the post smolts (Fig 3). Within the band the surface velocity component along the direction of the path (starting from the south) is estimated for May and June from 1996 to 2009 using the ocean model results (ROMS). Along the path the mean and max velocity is calculated in grid boxes, using a band width of 120 km and 25 km along the band. An estimated migration speed of 20 cm/s is used for the post smolts to swim from the release point to the nearest location in the defined path. From this location, the migration speed is calculated to match the time and location of recapture. Within each box the maximum and mean speed from the modeled surface velocity are calculated, and afterwards averaged over all grid boxes along the band from start to recaptured location (Fig. 4).

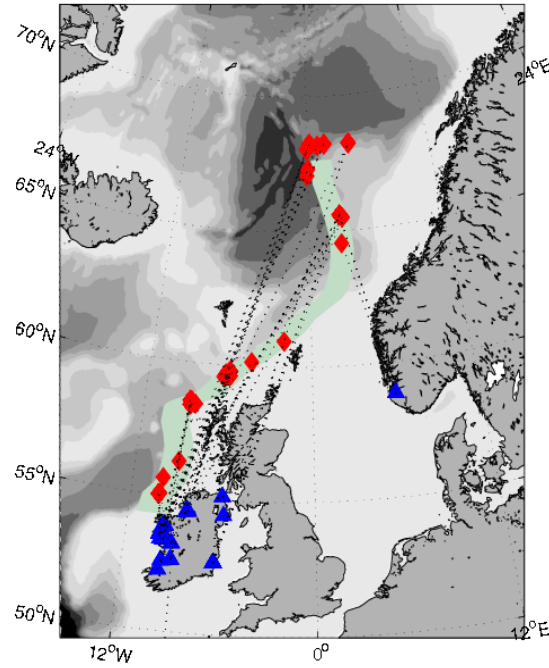


Figure 4. Release and captured locations of tagged fish. The defined migration route is indicated.

Generally, the migration speed is larger than the surface current, except for short migration distances. Based on these data we can therefore assume that the post smolts does not only drift passive with the ocean currents, but also has an active swimming. The difference between the migration speed and the surface velocities, which are the active swimming speeds, are in many cases about similar as the speeds from the currents. Using the averaged body length, between the release and recaptured locations, the swimming speed as function of body length is calculated. Figure 5 shows the swimming speed as function of bodylength for different travelling distances. The speed is less than 1.5 bodylength per second with largest speed for longer travelling distances. Since we are mainly interested in the migration of the longer travelling distance we use 1.5 body length per second which is also close to what Booker et al. (2008) used in their migration model (20 cm/s for 12.5 cm body length).

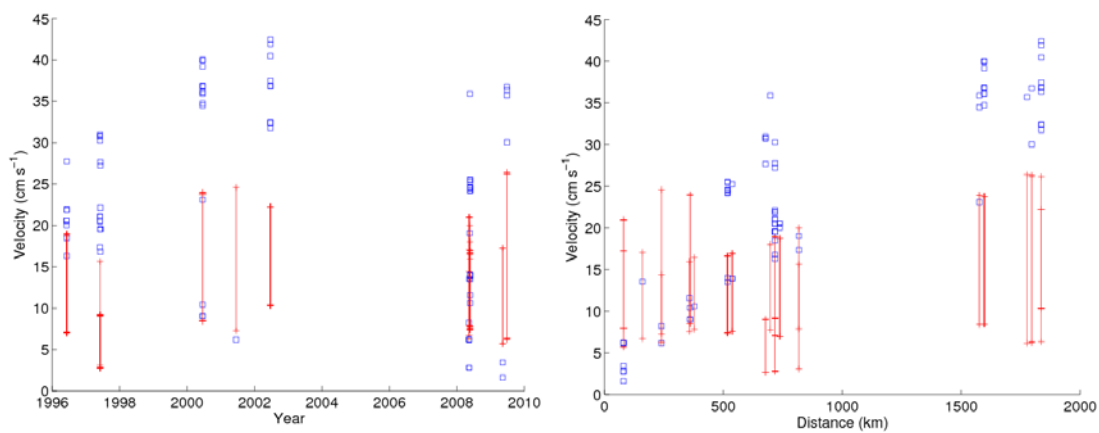


Figure 5. Velocity of migrated tagged post smolts (blue squares) and of averaged surface currents (max and mean) over similar distances as the migration path of the post smolts (red lines). Blue squares are total migration while red lines are surface currents from the model (maximum and mean values).

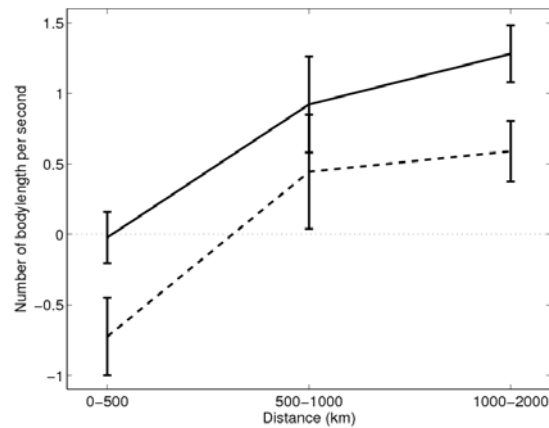


Figure 6. Active swimming speed of the migrated post smolts as function of body length per second. Solid line indicate for mean current along the defined path while dash line is for max velocity.

A simple post smolt growth model

A simple post smolt growth model is used to estimate the body length with time after the post smolt enter the sea. Using post smolt catches the body length increase was calculated to 0.6% per day (Figure 7).

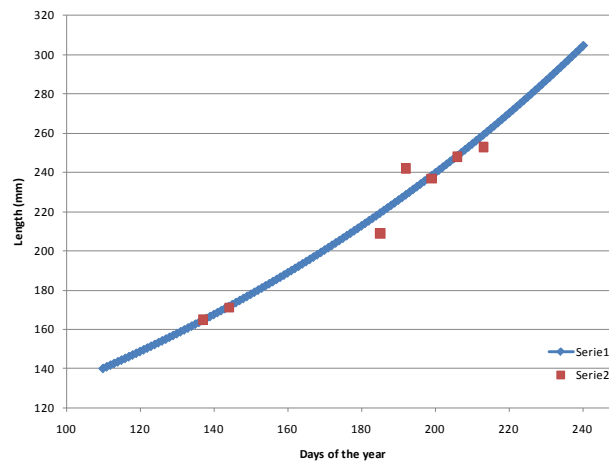


Figure 7. Observed length (red squares) and modeled (blue line). Blue line corresponds to 0.6% increase in body length per day.

The simulations

Two key regions of origin where defined, one southern stock and one northern stock (Fig. 8):

- 1) West of Ireland (56N, 9.5W), migration date centered at 1 May
- 2) Southwest of Norway (58N, 5E), migration date centered at 15 May

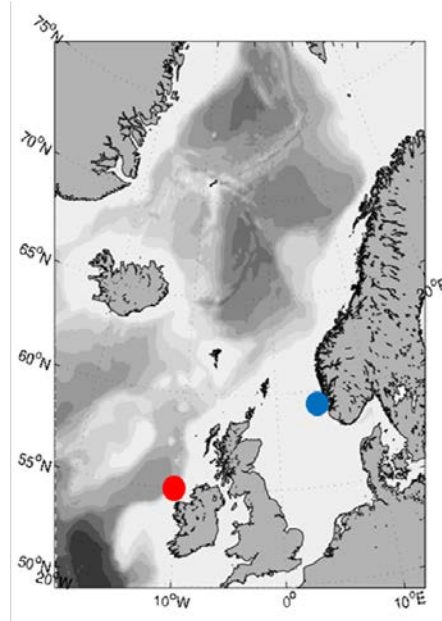


Figure 8. The two key regions where particles are released represent the southern (red point) and northern stock (blue point).

At these two locations 2000 particles are released, distributed over 3 weeks (Gaussian distribution, Fig. 9), and the simulations were done to the end of August the same year.

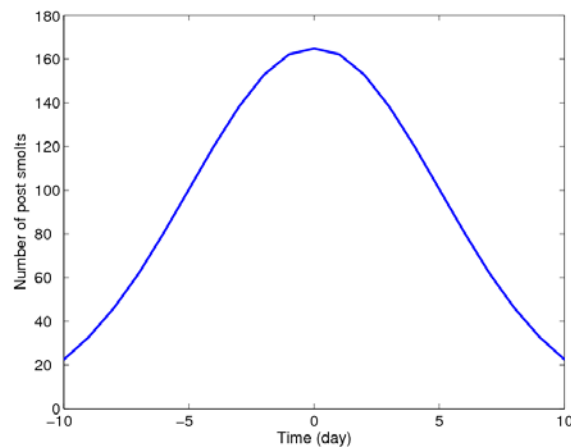


Figure 9. Distribution in time of number of released post smolts, where time=0 is the centered migration date (1 May for the southern stock and 15 May for the northern stock).

In the model we assume that the post smolts swim in the same direction as the current which seems appropriate according to the results from the tagged fish and also from the literature (e.g., Shelton et al. 1997). Also, the post smolts are found to prefer water within 8-12 °C (Friedland et al., 2000; Holm et al. 2004; Holst & Hansen 2000). In the model the post smolts are forced to stay within the preferred the temperature range (8-12 °C), and when outside the swimming direction is changed toward higher temperature using the horizontal temperature gradient.

In the open ocean post-smolts are mainly found in Atlantic Water, i.e. in water with salinities higher than 35 (Holm et al., 2003). Simulations with and without the preference of high salinity are performed. Two simulations were also done for two different years: 2008 and 2002. These years were chosen as the wind patterns were different (and then also the surface currents) and that the post smolts growth were different.

Model results

1. No preference for salinity

Southern stock, year 2008

Simulated trajectories are shown for 2000 particles that were released from 20 April to 10 May 2008 in Figur 10a. A concentration plot (Figure 10b) shows clearly the migration route. The post smolts migrate northward, some through the Faroe-Shetland Channel and some around the Faroese, to the northern Norwegian Sea.

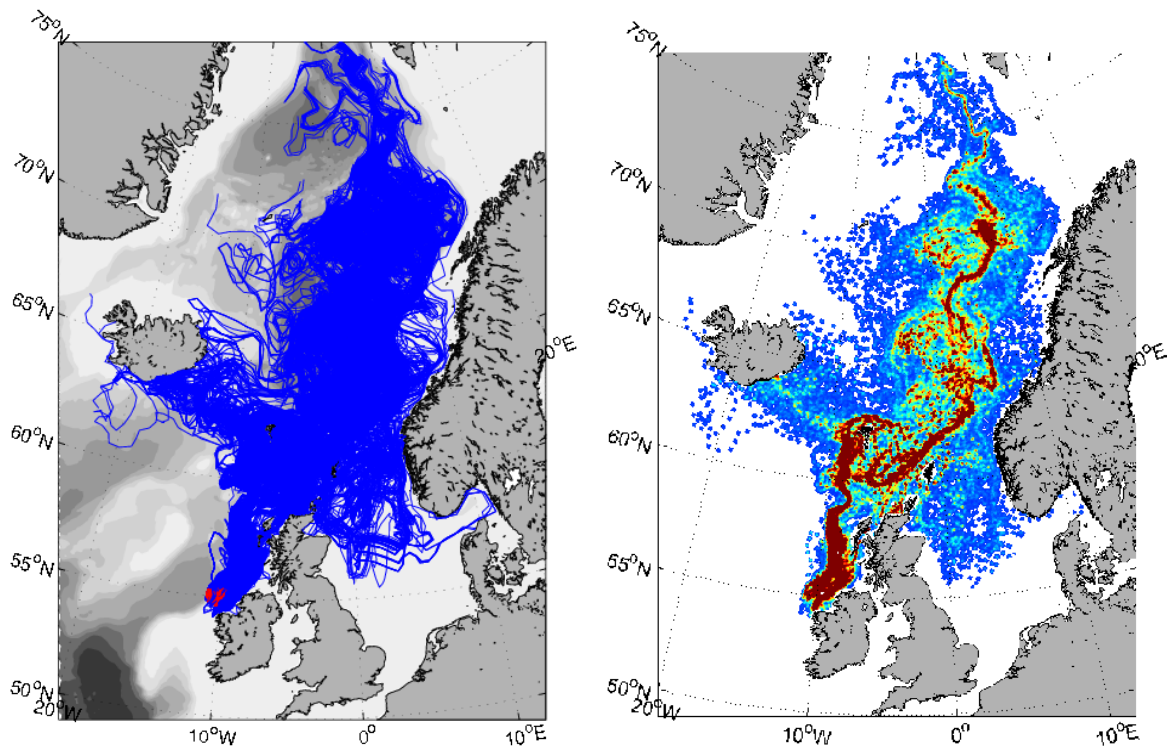


Figure 10. a) Left: Simulated post smolts trajectories to end of August 2008 (20 April – 31 August) and b): Right distribution map for the whole period (red colors indicate more than 5 particles)

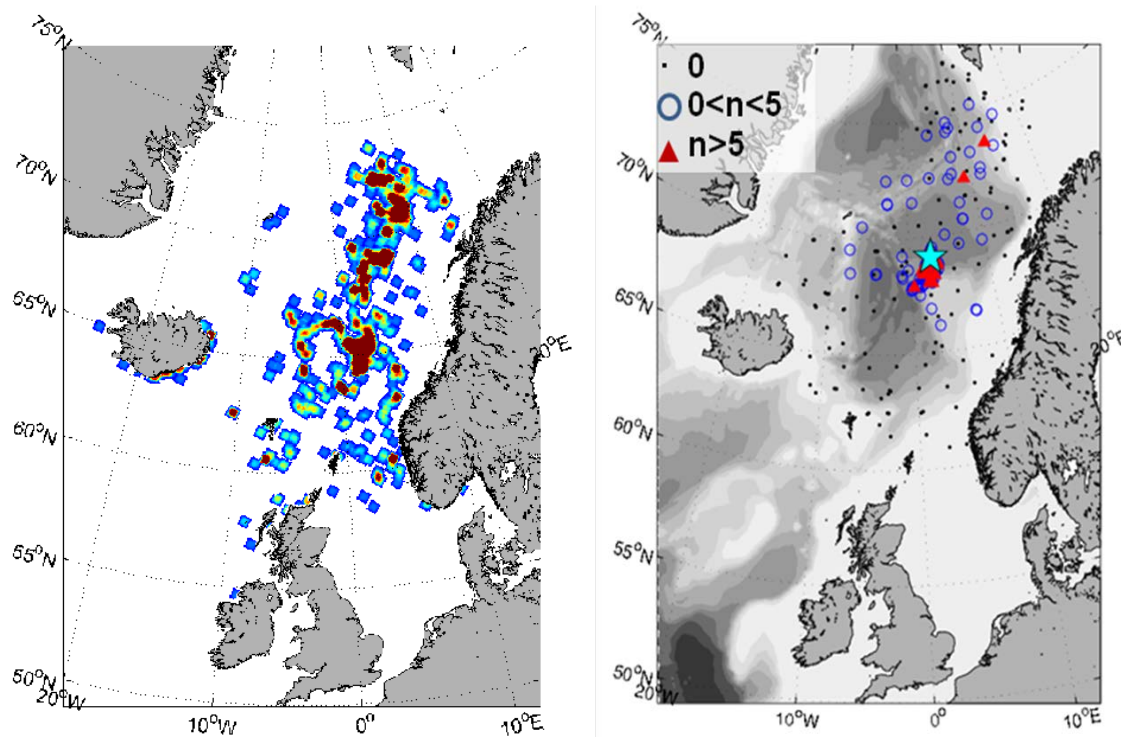


Figure 11. a) Left: Simulated distribution of southern stock (Ireland) in the early August. B) Right: observed distribution of southern stock for July/August for 2008/2009, using the genetic information (SALSEA-GRAASP).

There is generally a good agreement between the modeled and observed post smolt distributions for July/August 2008 (Figure 13). However, the modeled distribution has some particles in the southern Norwegian Sea that are not in the observations. This may call for a slightly modification of the migration drift model, e.g., increased swimming speed, or even an inclusion of mortality in the model. For the latter this might be a case for post smolts that have a less successful migration to the feeding area. The difference between the modeled and observed distribution might also be a result of too few observations in the southern area to measure the post smolts there at that time of the year.

Northern stock, year 2008

The simulations for the northern stock in 2008 show mainly a northward migration with some exceptions of a westward migration into the North Sea (Figure 12). Some of these latter exceptions continue also northward after some time. For this stock there is also a good agreement between the modeled and observed distribution, but here, as for the southern stock, there are some particles in the southern Norwegian Sea, that are not in the observations (Figure 13). The reason for this might be the similar reason as mentioned earlier for the southern stock.

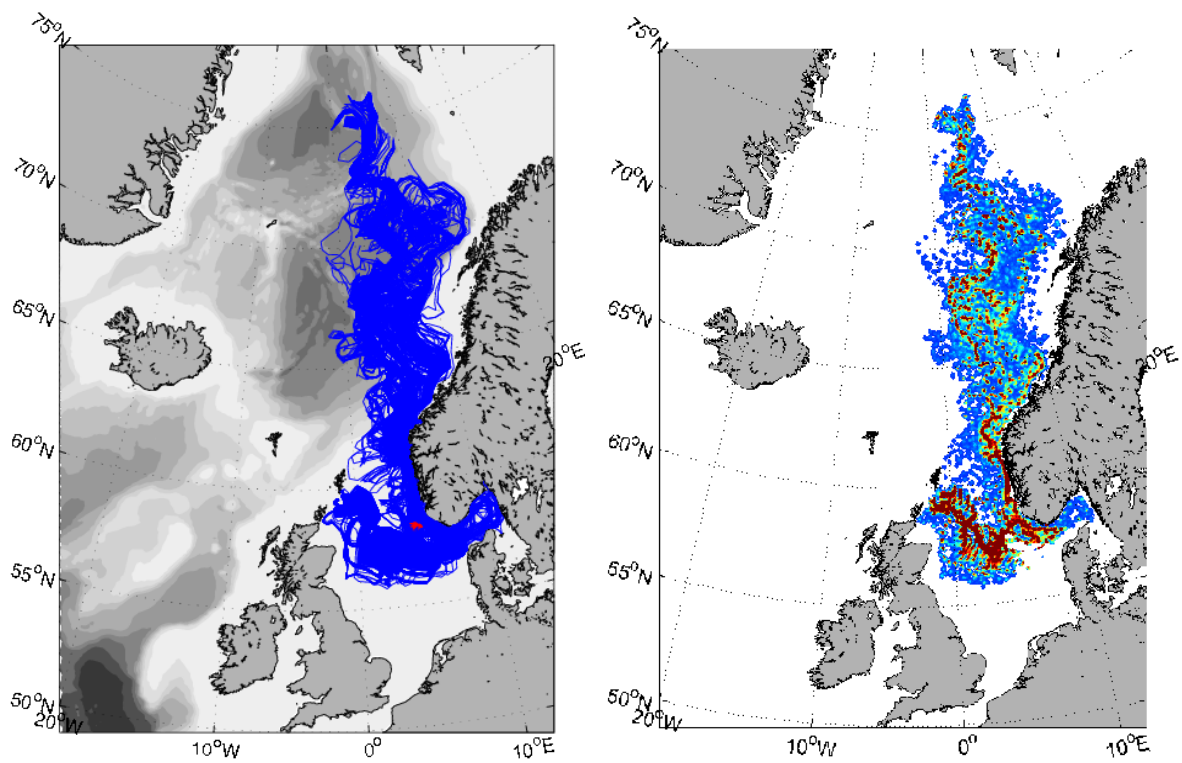


Figure 12. Simulated post smolts trajectories to end of August 2008 (20 April – 31 August) and concentration plots (red colors indicate more than 5 particles).

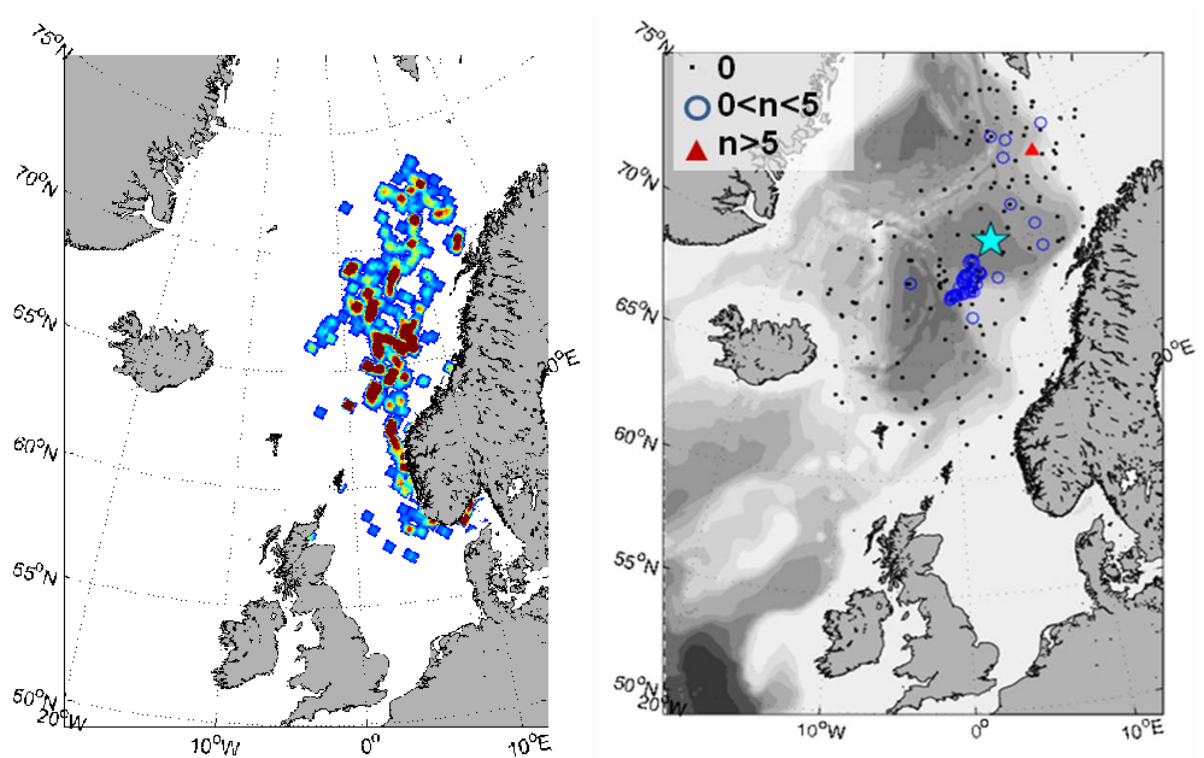


Figure 13. Left: Simulated distribution of northern stock (southwest of Norway) in the early August. Right: observed distribution of southern stock for July/August for 2008/2009, using the genetic information (SALSEA-GRAASP).

Southern stock, year 2002

I. No preference for salinity

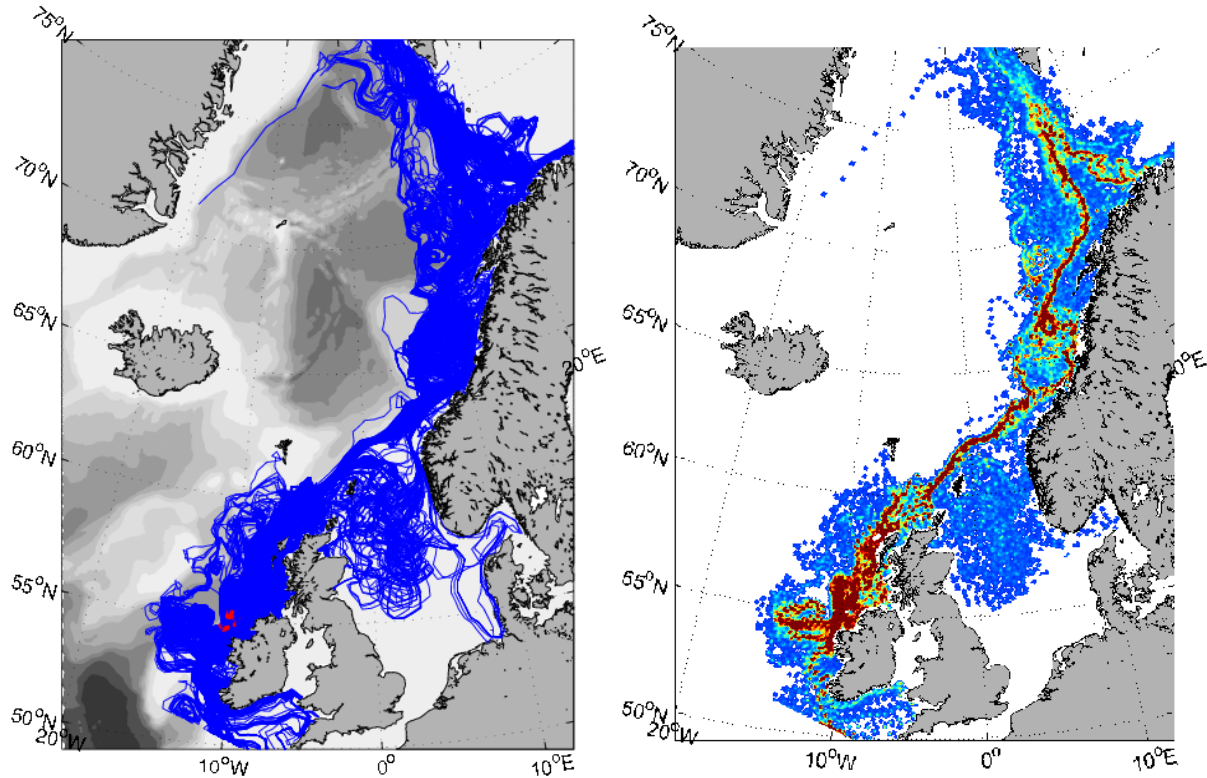


Figure 14. Simulated post smolts trajectories to end of August 2002 (20 April – 31 August) and concentration plots (red colors indicate more than 5 particles).

There is a big difference between the modeled migration of the southern stock in 2002 compared with 2008 (compare Figs. 14 and 10). In 2002 the migration pattern is much more eastern located than compared with 2008. Also, there is no simulated westward post smolt migration, around the Faroese or toward Iceland. The main explanation for this difference, between 2002 and 2008, is the difference in the ocean currents between the two years due to changes in the atmospheric circulation (i.e. wind pattern). At the surface, which the post smolts are mainly located, the currents are strongly affected by the wind, and periods with strong southwesterly winds (as in 2002) gives a stronger eastward surface current.

II. Preference for salinity

Post smolts have preference of saline water (Holm *et al.* 2004; Holst and Hansen, 2000). During estuarine migration swimming speed increased under conditions of a positive salinity gradient (Hedger *et al.*, 2008, 2009). A detailed analysis between the post smolt distribution and the salinity is given in WP5 deliverable D5.2. Based on that result and from the literature a salinity preference for the post smolts were included in the migration drift model. When salinity was lower than 35 the

swimming direction of the post smolt was in the direction of the positive salinity gradient (i.e. toward higher salinity).

Figure 15 shows the difference between an inclusion of salinity preference or not. When the particles move northward into the Norwegian shelf they follow a more western migration route to avoid the low salinity water that derives from the coastal current.

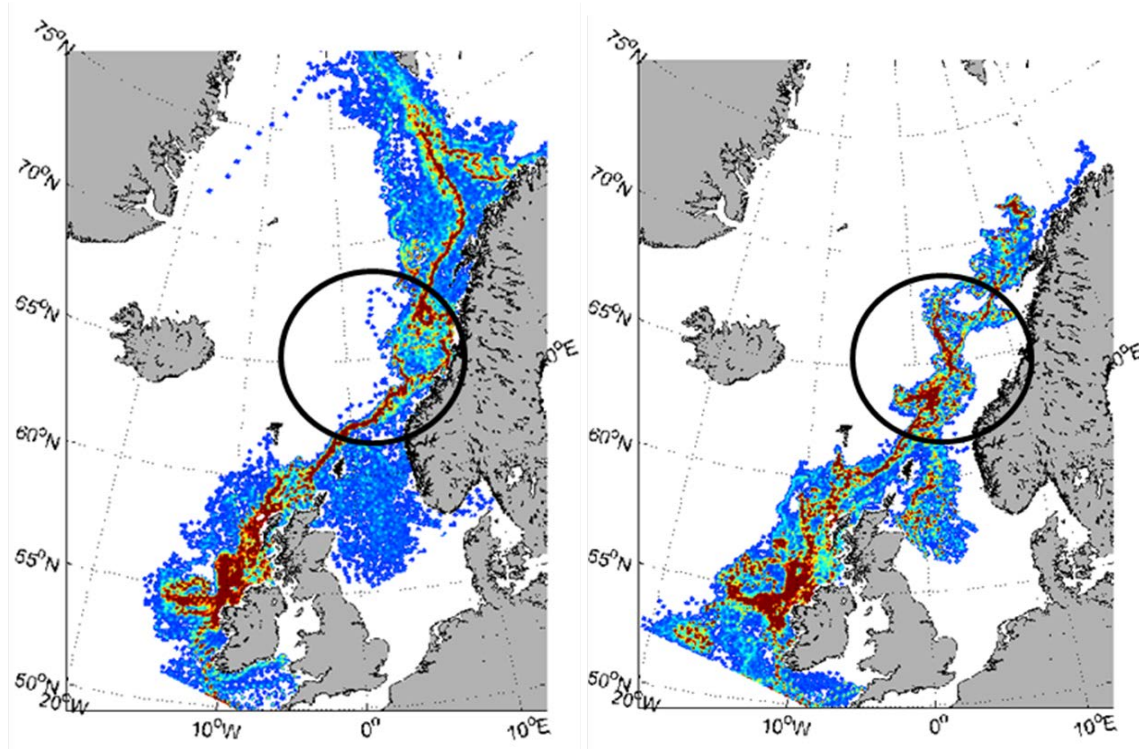


Figure 15. Concentration plot for southern stock without (left) and with (right) preference for salinity for 2002.

Discussion

The alteration of suitable migratory pathways has been suggested as a factor in the survival of North American post-smolts (Friedland et al. 1999) and should be considered for European stocks, as well. Migratory species are known to change routes in association with changing currents, temperature and salinity distributions (Minns et al. 1995; Ottersen et al. 2004), and habitat shifts in response to climatic alterations have already been reported for many species in the North Sea (Perry et al. 2005). An alteration in suitability of any of the habitats utilized will affect the population characteristics of a migratory species (Reddin et al. 1997) and may contribute to an alteration of the predator-prey relationship in addition to the direct energetic cost.

The simulations in this report show that the surface currents may alter the migration pathways for the two different years 2002 and 2008. In 2002 the direction of the currents was much more eastward compared to 2008 forcing the particles more eastward into the coastal areas of Norway. However, including a preference for higher salinity in the model will at least partly account for this difference in migration routes. Thus, salinity may be an important parameter for making decision of swimming direction. In 2008, several particles moved also westward north of Scotland and several migrated around the Faroese before moving northward in the Norwegian Sea.

There are also some important key areas in the migration pathway where pathway shifts may occur. One is North of Scotland where one direction is through the Faroe-Shetland Channel and one westward south of the Faroese. The other key area is in the southern Norwegian Sea where one branch is the continental shelf edge (the inner branch of the Norwegian Atlantic Current) and the other is northward, i.e. to the outer branch of the Norwegian Atlantic Current west of the Vøring Plateau. The migration routes for the different specific stock groups is showed schematic in Figure 16.

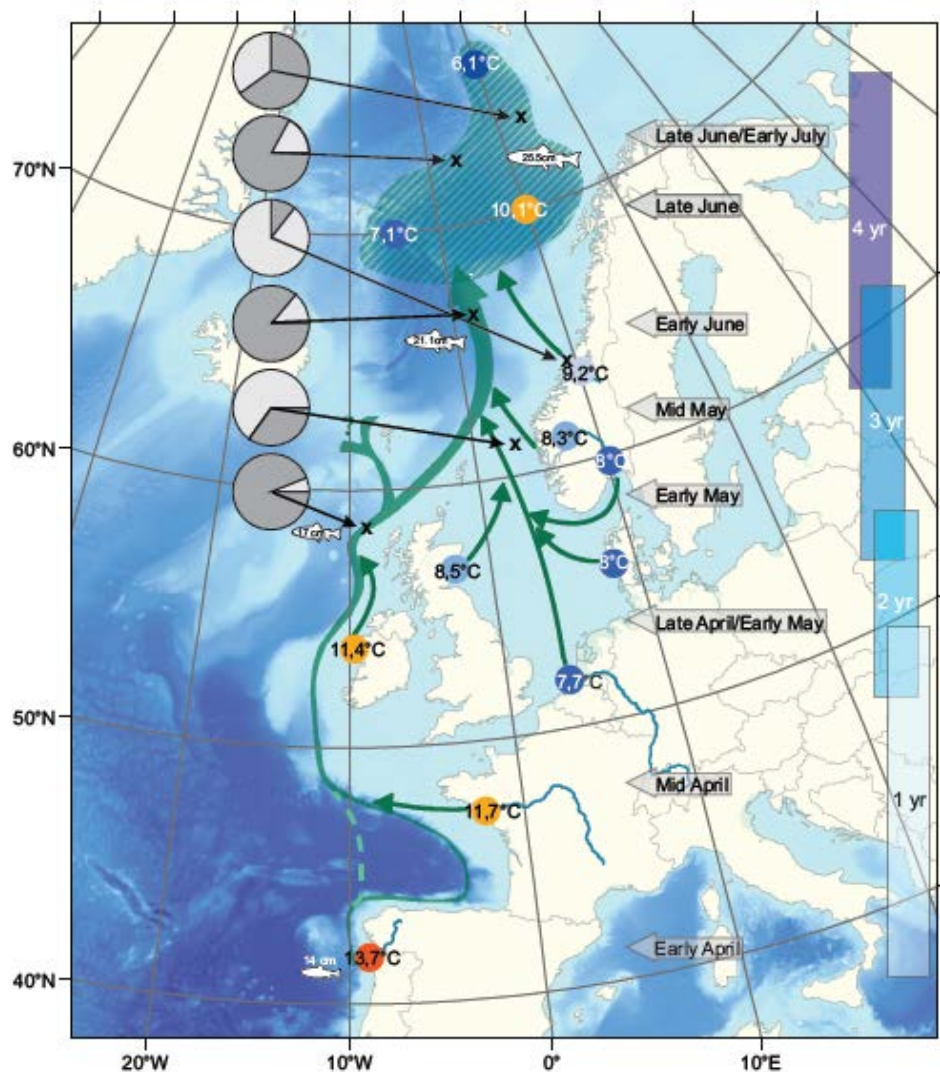


Figure 16. Schematic view of the migration routes for the different specific stocks based on the migration model and genetic assignment. Ambient sea surface temperature, timing of migration, smolt age, and the relation between the southern and northern stock groups are also shown.

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The conceptual ecological model

Introduction

The Atlantic salmon has been principally managed as a fish of fresh water whereas, in reality in the case of anadromous stocks, it is a fast moving pelagic marine predator for a large portion of its life-cycle. This is important as the potentially greatest threats the species now faces are in the ocean and research must rise to the challenge and recognise that these most fundamental of questions can only be addressed through a co-ordinated international programme. Unfortunately, at present, knowledge of the marine life of the salmon is rudimentary and inadequate. In particular, insight into migration and distribution is needed and fundamental to identifying factors underlying ocean mortality.

Many factors are known to interact and affect salmon mortality at sea (Figure 17). These include, for example, the carry over effects from freshwater, effects of aquaculture, and predation, something often not considered. Fortunately, some of these freshwater influences are being addressed by habitat protection and restoration programmes. At sea, some mortality factors are also being addressed such as the potential post-smolt by-catch in pelagic fisheries in the Norwegian Sea has been investigated by the Study Group on By-Catch of Salmon in Pelagic Trawl Fisheries (SGBYSAL, ICES 2004).

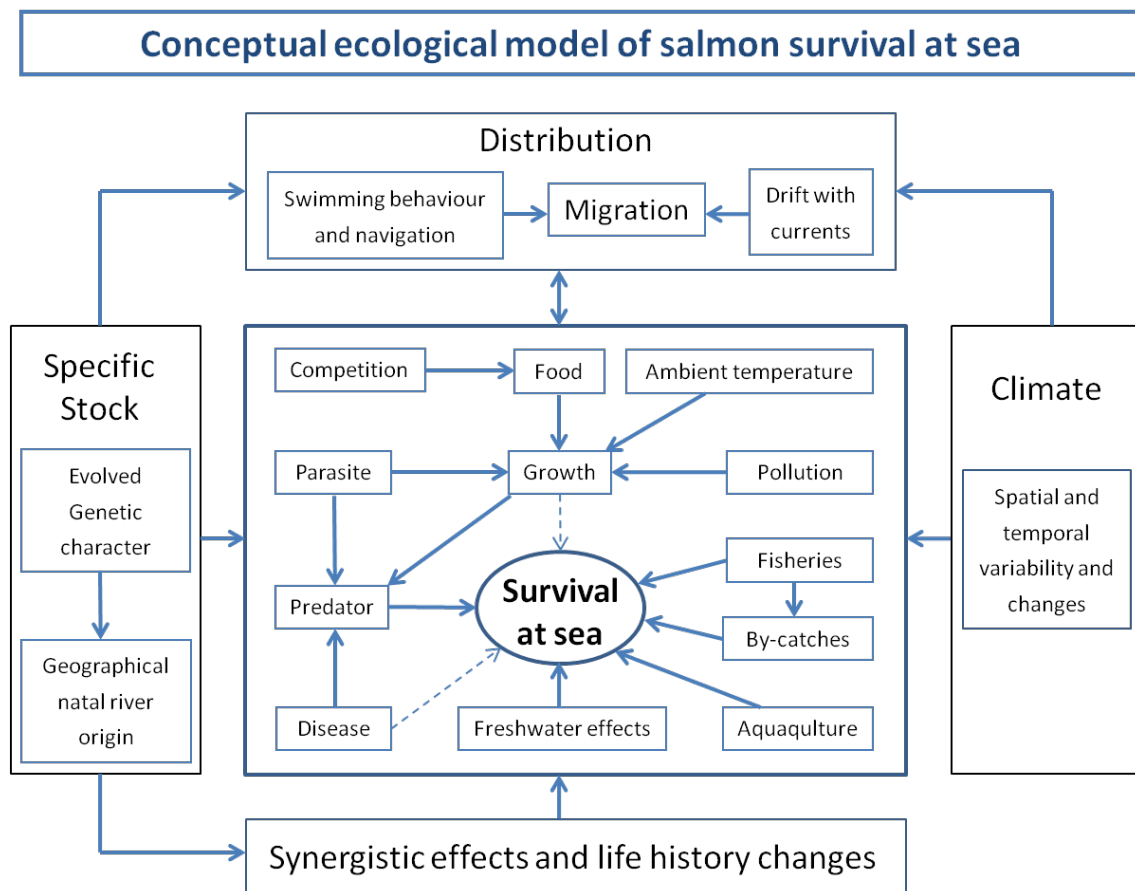


Figure 17. The SALSEA-Merge conceptual ecological model of salmon survival at sea.

The main response to the decline in salmon stocks has been through fisheries management measures and, in all salmon producing countries, determined efforts have been made to limit exploitation. Most directed commercial fisheries have been significantly reduced or closed in recent times - e.g. distant waters fisheries and many home-water mixed stock fisheries. However, the main outstanding problem confounding the expectation of increased returns following these management measures has been the continuing decline in marine survival. Obtaining information on the biological issues, **such as those listed below**, is critical to determine why stocks have been declining and whether further or new management action can be taken to mitigate the problem. These biological issues all relate to when, where, why and how salmon are dying at sea.

One of the key issues in increasing our understanding of the marine ecology of the species is to understand the differences which may exist between different regional stock groups and river/tributary populations in their ecology and distribution. This requires the ability to identify the origin of fish captured in the marine environment, which can be most cost effectively and comprehensively achieved using DNA profiling.

Ecological information on specific regional stock groups and river/tributary populations was generated during the project by the integration of information on the origin of fish, obtained from sampling (tagging and genetics), with environmental and other biological information collected during the course of the research cruises. The results of these analyses were then used to extend understanding the migration patterns of different genetic stock groups using the SALSEA-Merge particle drift model (Part 1 in this report). In turn the insights so gained provide the basis for the development of a more advanced ecological model linking e.g., growth performance, environmental conditions, and the distribution of food organisms. This part (Part 2 in this report) describes the main factors of the conceptual ecological model of salmon survival at sea as shown in Figure 17.

Main factors in the conceptual model

Growth

Factors: Food, Ambient temperature, Pollution, Parasite

1) Background

Atlantic salmon are remarkably eurythermal (Elliot, 1991) and feeding and growth typically are constrained to 4.9-26.7°C, but this narrows as food availability declines and growth therefore is determined primarily by prey, temperature and fish size (Brett et al. 1969). The distribution, mortality and growth of salmon in the ocean have been found to be related to sea surface temperatures (SST) (Reddin and Shearer 1987, Friedland et al. 2000, Friedland et al. 2009), although other factors like plankton food resources in the post-smolt nursery area are known to be important (Friedland et al. 2009). Faster growth during the post-smolt period results in lower accumulated mortality in a cohort, and hence, higher recruitment (Friedland et al. 2009). The optimum temperature for growth of Atlantic salmon in seawater is not known, although Handeland et al.

(2003) estimated it to be about 13 °C from rather sparse data on Norwegian farmed strains of post-smolts, and Smith et al. (2009) obtained a maximum of 14 °C from simulations with a bio energetic model. For juveniles in fresh water it has been estimated to be between 16 and 20 °C with food supply in excess, with food consumption peaking at 19-21 °C (Jonsson et al. 2001). However, the optimum temperature for growth decreases with decreasing food rations (Brett et al. 1969), and experimental data on behavioral thermoregulation by fish generally indicate that the preferred temperature selected by fish seems to be similar to the temperature yielding optimal growth rates (Jobling 1981). Hence, temperature preferences at sea may be considerably lower than that optimal at excess rations (Welch et al. 1995). Most post-smolts caught by floating trawls in the Norwegian Sea during summer (May-August/September) were captured at sea surface temperatures between 8 and 11 °C (Holm et al. 2004). In the Baltic Sea, Alm (1958) reported that feeding salmon avoided water temperatures above 11-12 °C. In the same area, Jutila et al. (2005) observed increased survival rates of Atlantic salmon post-smolts when SST in June increased up to 12 °C, and then decreased at higher temperatures.

Studies of the diet of post-smolts in fjords (Rikardsen et al., 2004) as well as at their feeding areas in the Northeast Atlantic (Haugland et al. 2006), suggest that different crustaceans and in particular marine pelagic fish larvae such as sandeel and herring are preferred as prey. However, a substantial spatial and annual variation in prey diversity and feeding intensity has been observed. During autumn, hyperiid amphipods of the genus *Themisto*, euphausiids and mesopelagic shrimps have proved to be important sources of food for salmon in the Northeast Atlantic, shifting to various mesopelagic fish as lantern fishes, pearlsides and barracudinas during the late winter period (Jacobsen and Hansen, 2001). Large salmon (3-SW) tended to be more piscivorous than smaller fish. Haugland et al. (2006) observed unusually large quantities of 0-group herring in stomachs of post-smolts in the Norwegian Sea in summer 2002, and this coincided with a high condition factor and growth rate of post-smolts that year. In addition to availability of food, the energy content of the different prey species is important for growth.

Diseases and parasites in wild populations of Atlantic salmon has been reviewed by Bakke & Harris (1998). They concluded that few pathogens have caused significant disease epidemics in wild, and although parasites of returning adults are best documented, diseases among parr (e.g., *Gyrodactylus salaris*) are probably most important. Further, they concluded that the greatest diversity of parasites is known from the marine phase but few are likely to be significant pathogens. Since the late 1980s, however, there have been several reports of sea lice epizootics on salmonids in Norway, Scotland and Ireland, and in more recent years also in Canada, and it has been suggested that the apparent increased infection rate is correlated with the presence of salmon farms (Finstad et al., 2011). Infected post-smolts are expected to suffer from higher osmotic stress, and hence experience lower growth and be more vulnerable to predation than uninfected individuals.

Different kinds of pollution in freshwater and in estuaries may have negative effects on growth and survival of Atlantic salmon at sea. Both acidification (aluminium) and pesticides affect the spawning activity and spawning success of adult salmonids, as well as the survival of egg and larvae. Furthermore, freshwater contaminants can have delayed effects, for example, by affecting smolt quality, and thereby smolt-to-adult survival in sea water. I.e., the fish experiences the dose while in fresh water, but the ecologically relevant responses to that dose first emerge after the individual has entered sea water, which misleadingly might suggest marine causes (Rosseland and Kroglund 2011).

2) Main findings from SALSEA-Merge

Using contemporary digital scales reading techniques, marine growth rate of Atlantic salmon may now be estimated at short intervals; weeks for post-smolts and months for adult salmon. Applying intercirculi distances in scales as a proxy variable of growth rate, the results from post-smolts sampled in the Northeast Atlantic suggest that marine growth rates varied among years, with highest growth rates in 2002, followed by 2003 and 2009, and lowest growth rates in 2008. Both age structure and number of marine circuli in the scales suggest that the majority of the post-smolts caught belong to populations of southern European origin. Also, the first marine intercirculi distances were narrowest in one year old smolts, successively increasing with smolt age, indicating that growth rates during the first period at sea were lowest for salmon of southernmost origin. Merging growth data with genetic assignment confirms that most individuals were of southern origin, and the majority was assigned to UK and Ireland. Further, growth rate was lower the first weeks at sea in individuals from Spain and France than from UK and Ireland, and higher in individuals from Denmark (Fig. 18). Also, growth rates in this period were slightly higher in individuals assigned to North at the genetic Level 1 than those assigned to South.

Over 23,000 scales of adult Atlantic salmon from seven rivers located in six countries have been analysed using contemporary digital scale reading techniques. No clear temporal pattern in growth was observed for the two Scandinavian and one of the Icelandic rivers, while growth increased during the study period in the second Icelandic river. In stark contrast to this, the Burrishoole data (Ireland) indicate strong temporal variation over time with most recent years values being the lowest in time series. The lack of temporal synchrony between the seven rivers, which are widely located geographically, may suggest very different post-smolt feeding areas, which are influenced by different oceanic conditions and biological parameters. Growth was, however, clearly linked to oceanic conditions (either SST or NAO or both) for all rivers.

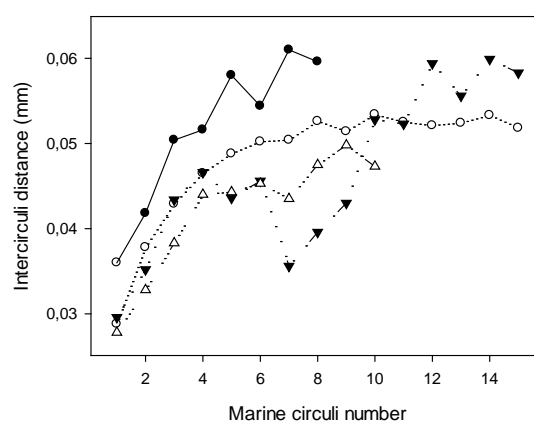


Figure 18. Intercirculi distances (mm) in the marine zone of scales of Atlantic salmon post-smolts collected at the 2009 surveys, assigned to South at Level 1, and further assigned at Level 3 (at 70% cut-off). Data are for () Denmark, () UK and Ireland, () France and Spain.

The main food of salmon are juvenile fish and *Themisto* spp. Salmon, herring and mackerel have overlapping diets, but herring and mackerel are specialized on *Calanus finmarchicus*. Salmon very rarely eat that prey. The diet of post-smolt salmon differs among year. In 2002 and 2008 juvenile herring and seabastes dominate the diet, while in 2003 and 2009 *Themisto* is the main prey.

Forage ratio and condition of the salmon was highest in 2002 and 2003 (Fig. 19). There were no clear differences in condition factor and forage ratio between 2008 and 2009 in salmon, herring and mackerel. Both condition factor and growth as calculated from the scales are related to the forage ratio of the salmon. Higher post-smolt salmon forage ratio and condition was not found during years when they were mostly feeding on fish.

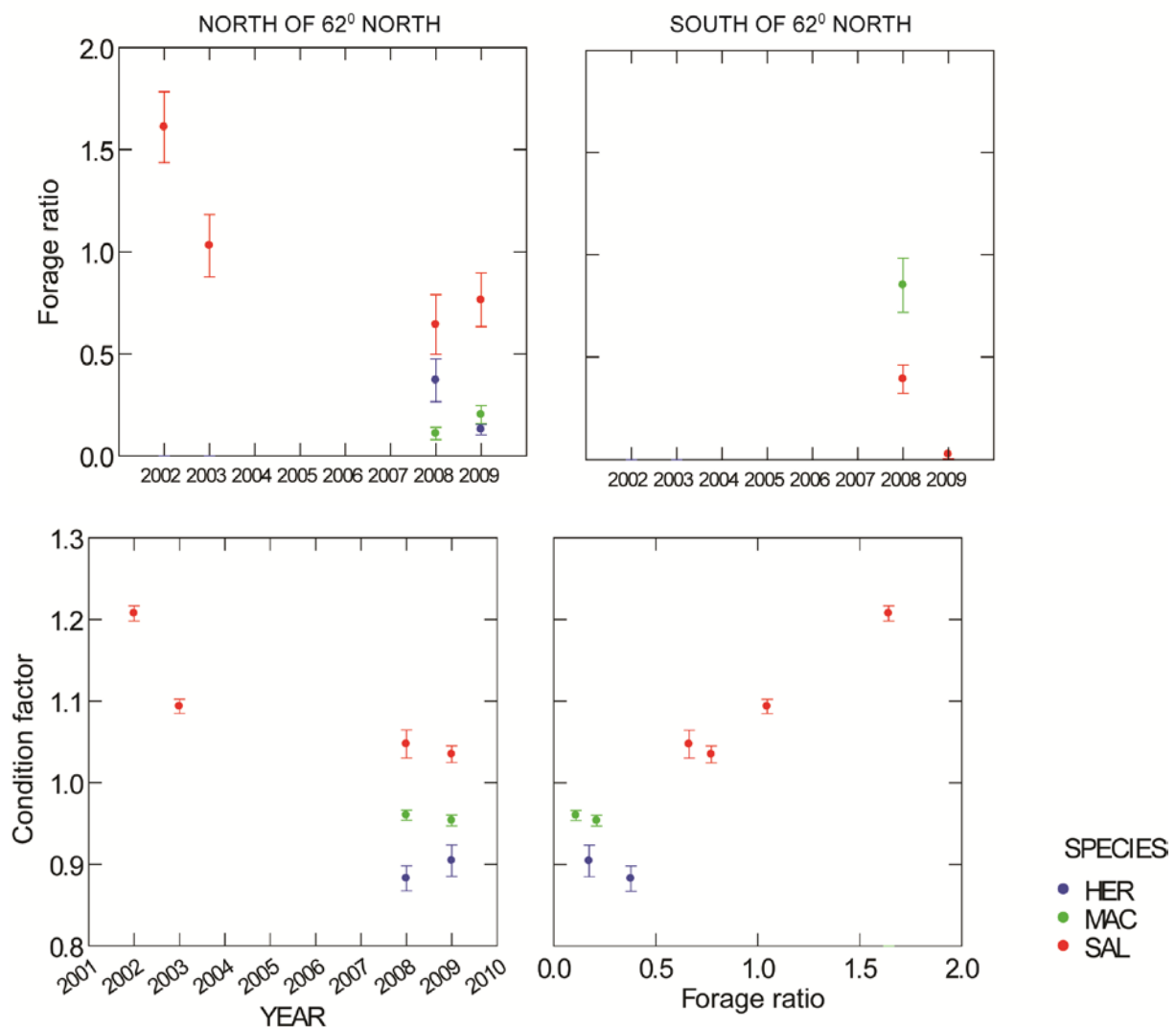


Figure 19. Forage ratio and stomach content of salmon, herring and mackerel in 2002, 2003, 2008 and 2009, north and south of 62°N (upper panels). Condition factor of post-smolts vs. year and FR, north of 62°N (lower panels). Average and standard error of the mean.

3) Summary/importance/gaps

Using contemporary digital scales reading techniques, marine growth rates of Atlantic salmon can now be estimated at short intervals. Hence, weekly growth rates have been compared

for post-smolts from different geographic regions, during the whole migration period from they left freshwater until they arrived at their feeding areas in the Northeast Atlantic. Most post-smolts captured in the Northeast Atlantic belonged to the southern component of the Atlantic salmon stocks, and within this group growth rates decreased from north to south, suggesting highest mortality during this life stage in the southernmost populations. Forage ratio was positively related to both condition and growth of post-smolts, showing the importance of good feeding conditions to growth and probably survival. It is still not known how feeding is related to food supply. The time series of marine growth analysed from scales of adult fish among seven populations which are widely located geographically, may suggest very different post-smolt feeding areas, which are influenced by different oceanic conditions and biological parameters. In contrast to the more northern populations, post-smolt growth declined substantially during the most recent years in the Irish population, which is of concern.

Predation

1) Background

Predation is probably the most important source of mortality in Atlantic salmon at sea, though diseased fish likely get eaten before they perish and thus never get recorded. Friedland et al. (2000) suggested that growth-mediated predation is the dominant source of recruitment variability in Atlantic salmon due to the implicit linkage between growth and survival demonstrated. Anthony (1994) discussed predatory birds, fish and mammals as sources of marine mortality in salmon. The main predation is believed to take place at the post-smolt stage, the first months after the smolts leave their home rivers. This is based on the assumptions that small fish are exposed to a larger range of predator species than large fish, and that there are more predators inside the continental shelf than in oceanic areas. LaCroix (2008) found very low survival in the estuarine zone in some Bay of Fundy stocks and acoustic studies confirm a strong negative trend in mortality per distance from the river mouth outwards (eg. Torstad et al., 2007) suggesting that even the very early marine phase may be a major bottleneck to many stocks.

Most studies on predation on salmon comes from coastal or near coastal areas spanning various predators like for instance cod (Hvidsten & Møkkelgjerd, 1987; Hvidsten & Lund, 1988), gannets (Montevecchi et al., 2002) and seals (Pierce *et al.*, 1991). Open ocean studies seem rare and the overall knowledge on predation on salmon in the open ocean is limited. Indirect studies can indicate sources of marine mortality using external damage in returning fishes (Thompson and Mackay, 1999) but will probably be biased towards certain predators.

The balance between the mortality of a year-class during the early marine phase and it's growth-mediated predation mortality during the later phases of the marine migration must be a key for understanding the large variations sometimes observed in year specific survival of salmon stocks of even near geographic proximity.

2) Main findings from SALSEA-Merge

Assessment of marine predation on salmon was not a goal for SALSEA-Merge and the project has no direct results on this issue. However, SALSEA-Merge has widened the knowledge on marine life of salmon significantly and has validated several hypotheses on salmon marine ecology and migration essential for assessing the effects of marine predation in future studies on the subject.

3) Summary/importance/gaps

There is a large gap in systematic knowledge on oceanic predation of salmon throughout its distribution and from all its predators, in particular during the open ocean migration. Large scale directed studies on predation of salmon seems unrealistic because of the costs involved and the main potential for progress in this field is suggested to be studies of overlap between large scale distributions of different stocks and ages of salmon and known overlapping predators. There is a great potential in exploring further already available data in this field and progress could be expected given more effort is put into such studies. Marine predation is a key element in understanding variations in salmon stock productivity on a temporal and geographic scale and deserves more focus. Results from such studies will be important input to the future marine ecosystembased management models which is expected to give important input to the overall management of Atlantic salmon stocks.

Fisheries

1) Background

Historical fishery for salmon

A number of countries have had major tagging programmes on salmon smolts in home rivers and adults in rivers or at sea. Many tagged salmon were recaptured in the high seas fisheries developed in the 1960s and 70s, when an important commercial long line fishery took place north in the Norwegian Sea in February-May. Tag recaptures from this oceanic fishery and recaptures in homewater fisheries of salmon tagged in the Norwegian Sea showed a mixture of stocks from UK, Sweden, Russia and Norway present in this area with a dominance of Norwegian salmon. 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). Fishing for salmon in oceanic areas in the Atlantic has declined considerably and is almost inexistent in recent years.

Bycatch of salmon in oceanic fisheries

Reports of salmon being taken during pelagic commercial fishing operations for a number of fish species in the eastern North Atlantic had been circulating for decades, but these were sporadic and often anecdotal in nature and did not provide evidence of any potentially significant by-catch of salmon in these fisheries.

However, in the late 1990-ties, high numbers of Atlantic salmon post-smolts were taken in surface trawls together with large catches of mackerel in a Norwegian research fishery for salmon in the Norwegian Sea (Holm et al., 2000). These catches indicated an overlap in time and space with the oceanic mackerel fishery and the post-smolt migrating to their northern feeding grounds, resulting in a potential risk for salmon to be taken as bycatch in commercial pelagic fisheries, the mackerel fishery in particular. This did also raise the possibility of salmon being intercepted by fisheries for other pelagic species such as herring. Accordingly, in 2002 NASCO asked ICES to “provide an estimate of the bycatch of salmon post-smolts in the pelagic fisheries based on the scientific information currently available” (ICES 2002). The request was addressed by the Working Group on North Atlantic salmon (WGNAS) at several meetings. Due to the extremely wide range of estimates, from less than 20 – over a million post smolts taken, found in the ICES reviews (ICES 2002, 2003), a specific Study Group on Bycatches of Salmon in Pelagic Fisheries (SGBYSAL) was convened in 2004 and 2005, with the task of collating and analyzing available information on this topic and providing an estimate of the bycatch of salmon in pelagic fisheries. Two reports presenting the status of knowledge were produced (ICES 2004, 2005). These concluded a.o. that there were areas where clearly the spatial and temporal overlap between post smolts and pelagic fisheries existed, but the magnitude of the bycatches could not be estimated due to lack of disaggregated data on captures (ICES 2004). In 2005 such data were provided to the group, and a wide range of estimates were calculated based on salmon trawl research data, observer based screening of catch samples on board commercial ships and registrations from fish factories on ships and on land (ICES 2005). However, the conclusion of the group was, that in absence of reliable research data from large scale commercial operations, the best estimates would be the ones based on Russian records from fish factory vessels where all fish landed are handled manually before packaging and freezing. These data yielded low estimates for post smolt bycatch. It was also concluded that greater understanding of the many factors underpinning stock status in salmon is necessary in order that advice can be given to managers to appropriate the necessary actions to conserve and if possible enhance stock status (ICES 2005). Lately, new information from Icelandic and Faroese screenings of samples from catches delivered at land based factories and occasionally from the Norwegian reference fleet, show that also adult salmon are taken in various types of fisheries, but predominantly in pelagic operations. These data suggest that the bycatch issue might be of greater importance than could be confirmed by the SGBYSAL group

2) Main findings from SALSEA-Merge

Neither salmon fishery nor bycatch issues were a scope for SALSEA. However, through the new knowledge gained from SALSEA-Merge, the distribution of post smolts of different origin in the NE Atlantic is far better understood, and the “risk areas” where interception may occur can now better be assessed.

3) Summary/importance/gaps

The novel information on the distribution of young salmon from different regions may significantly improve the potential for avoiding interception from the pelagic fisheries, e.g. by enabling recommendations for closed areas, closed times, depth regulations of trawl fisheries, etc. during the transition of post smolts through the main fishery areas.

The largest gap in knowledge regarding interception of salmon in other fisheries relates to the level of mortality of those individuals who pass through commercial fishing gear without being captured (non-catch fishing mortality). This issue is far beyond the SALSEA-Merge span, and can only be solved through scientifically controlled fishing experiments with commercial gear types.

Specific Stock

1) Background

The wide geographical distribution of anadromous Atlantic salmon spawning rivers (Figure 20), by itself, dictates that each river stock will encounter a unique set and sequence of conditions during the marine phase of its life-cycle. This arises due both to the spatial location at which the marine journey commences and ends as well as the fact that the timing of sea-entry varies with temperature and latitude, from early April in the south to June in the northern latitudes of the species range; this can also vary within a river stock (e.g. Stewart et al., 2005). The same is also true for river return, where sea-age is also a factor with 1SW fish returning later than 2SW and older fish (e.g. Stewart et al., 2002). However, the full extent of this timing variation within and among river stocks is only partly known (Webb et al., 2007). What is known is that timing is dictated by environmental conditions (e.g. Jonsson and Ruud-Hansen, 1985) as well as by the species evolutionary background, varying heritably among at least some if not all river stocks (e.g. Nielsen et al. 2001), and can even vary among breeding populations within a river (Stewart et al., 2002, 2006). The full extent of this variation is as yet uncertain as is its influence on marine mortality.

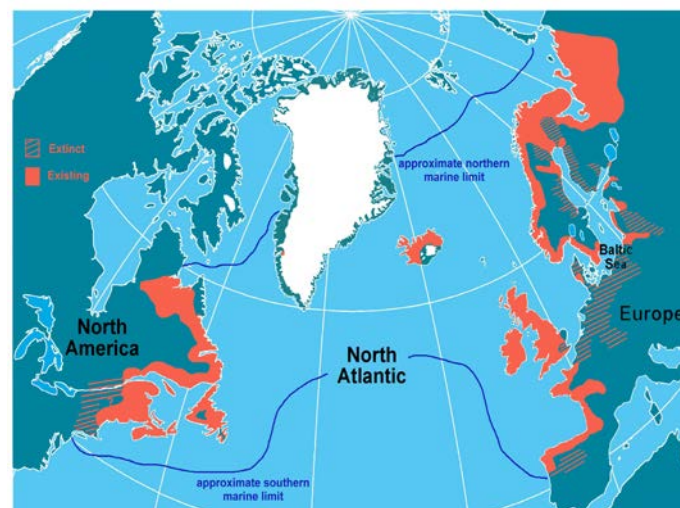


Figure 20. Map showing the approximate terrestrial and marine distribution of Atlantic salmon (*Salmo salar*) in the Northern Atlantic Ocean

Geographical origin and time of marine entry also, almost certainly, influence the route and extent of a river stocks marine migration e.g. main feeding areas used. However, this will also be conditioned by other factors. Primary feeding areas, and the routes chosen to get there, will also in part be

dictated by contemporary marine conditions; fish are unlikely to stay/survive in areas where there is no food or have unacceptable oceanographic conditions. At the same time, it is also clear that migratory routes and destinations can also be substantially influenced by a river stock or population's evolved genetic character. This can be inferred from the general spatial heterogeneity in general patterns of tag returns over the years from rivers in different regions, though these clearly show considerable spatial and temporal overlap as well (Hansen and Jacobsen, 2000; Holm et al. 2003). For example, tagged North American and Icelandic salmon are absent from the Northern Norwegian and adjacent Barents seas, a key feeding area for more local salmon stocks. A more extreme example is that of the Inner Bay of Fundy salmon stocks in North America where historical tagging work shows that with one notable exception, the salmon from rivers in this area do not go to northern seas around West Greenland to feed (Webb et al., 2007) but rather appear to feed more locally in the Outer Bay and the Gulf of Maine. Combined with this they have a unique life-history pattern of high levels of repeat spawning and have over the last decades suffered much larger declines than adjacent Outer Bay stocks. In the Baltic, behavioural genetic analysis shows distinct migratory patterns for stocks from different sub-regions within the Sea (reviewed in Webb et al., 2007). Little is known about the importance of heritable stock differences in stock migration patterns aside from these limited and geographically restricted insights.

2) Main findings from SALSEA-Merge

Application of the GRAASP to the historical and contemporary set of assembled salmon catches from the NE Atlantic provide a more general and broad-scale confirmation of the existence of variation among regional European stock groups in their temporal and spatial patterns of marine migration. The distribution of broad-scale regional stock groups is demonstrated to be non-random. In the area covered by the samples analyzed, northern regional groups, including those from Iceland are significantly under-represented compared to expectations based on river productivity, indicating that the marine areas for these stocks are spatially and temporally different to a significant degree; this is in accord with less extensive and more intensive analysis of tag returns across the years from hatchery stocks from index rivers across Europe. In particular, the analysis of salmon from waters around Iceland show that only a very small proportion of these are from Icelandic rivers, as was the case for samples from elsewhere. Thus the main marine areas for Icelandic salmon, as well as the more northerly stocks from Finnmark, the Kola Peninsula, and White Sea, were not identified; the latter are likely to center their marine distribution in the Barents Sea, an area not included in the study.

3) Summary/importance/gaps

Considered collectively, the existing evidence provides compelling support for the existence of biologically important variation in migration patterns among regional stock groups and individual river stocks, most likely driven by a combination of geography, evolutionary history, or contemporary oceanographic conditions. In turn, this makes it difficult to envisage that such variation is not a factor in the nature and extent of marine mortality. The genetic work carried out demonstrates the clear potential for using genetic markers of region/river of origin, as implemented in the GRAASP, to develop an extensive detailed picture of the migratory differences among regional stock groups and individual river stocks. The preliminary study carried out demonstrates this potential and provides

compelling evidence of differences at the regional stock group level. However, the limited spatial and temporal scope of the samples precludes the development of a complete and detailed picture of these differences. To achieve this, the GRAASP needs to be applied to a much more temporally and spatially extensive set of samples.

Synergistic effects and life history changes

1) Background

Life history variation of potential importance to survival of Atlantic salmon in the marine environment occurs within and among populations e.g. in smolt age and size, timing of smolt migration, age and size at first age of reproduction (age of male maturation, timing of river entry, timing of spawning, propensity for repeat spawning, egg size, egg number, migratory versus non migratory, homing versus the tendency to stray (Webb *et al.* 2007). The evolution of traits and prevalence of the form of a given trait with respect to another can at least in part be expected to be linked with spatial and temporal variability in the nature and harshness of the ocean environment. The variations in important traits will be maintained in the population through balancing or frequency dependent selection as the advantage changes back and forward in a constantly dynamic environment. This makes such quantitative variation essential for long-term population viability and from a fisheries management perspective for maintaining productivity (Hilborn *et al.* 2003; Schindler *et al.* 2011).

Timing of smolt migration is a particular example and is likely to be optimized for fish to enter the sea when food has historically been most abundant along a stock's migration route (Kennedy & Crozier, 2010). Older and bigger smolts have a better survival in the sea than younger, smaller smolts (Crozier, 2003), but must trade-off the accrued advantage of larger size with the chances of surviving additional winters in the river. Conditions in the sea can be so severe that the abandonment of the marine phase part of the life cycle becomes a necessary strategy for survival (Power, 1969). Similarly it is better to mature as a parr if the chances of survival at sea and return as a sea run adult are poor. Age and size at maturity and the propensity for repeat spawning are trade-offs between the benefits of staying out longer at sea and coming back bigger, with more and bigger eggs set against the chances of not coming back at all. So as the environment (here the marine environment) changes, the trait or phenotype will, at least in theory (Gomulkiewicz & Holt, 1995), evolve to track that change, in order to optimise fitness under the conditions prevailing. Sometimes these traits work in synergy, sometimes as they evolve they are antagonistic to each other.

The relationship between the marine environment and variability in life history can be seen in details of studies in Scottish rivers where the sea age at maturity, and the seasonal return time have shown considerable fluctuations over the past 200 years (Summers, 1995). The ratios of the sea age and run-time phenotypes typically alternate considerably but the relative abundance of these trait types shows high levels of coherence among rivers and among seasons (Youngson, 2002). Bacon *et al.* (2009) surmised that the common trends over years documented between sites, and the coherent annual differences from several of these, hinted at broad, common causes in the ocean. These could have environmental (Friedland *et al.*, 2000, 2009) and genetic components (Garcia de Leaniz *et al.*,

2007); and could include the direct effects of human fisheries and their delayed, and, potentially, even evolutionary, consequences (Hard et al., 2008, Bacon et al., *in review*). A study by Bacon et al. (*in review*), however, finds little evidence that heritable processes were involved in either the decline in mean mature-length or the return-date seen in recent years.

The classic paradigm for Atlantic salmon at sea considers that post smolts disperse with the aid of ocean currents (Bacon et al. 2009; Booker 2008; see also the section “Distribution”). It implicitly assumes that any smolt from any particular river could become either a 1SW or a MSW fish and whereby faster-growing fish might become 1SW fish, whereas slower growers would be obliged to stay at sea longer before reaching a breeding threshold, and thus return as MSW fish. However, attempts to reconcile such growth concepts with the quantitative details on the findings derived from a very large dataset on sea age, seasonal, and sex-difference (Gurney *et al.*, 2008), suggest that these random ocean dispersal and growth based models were overly simplistic. However, there is a more plausible explanation for the emerging patterns of cyclical increases and declines of sea age and freshwater return date observed in their data (Bacon et al. 2009). Youngson (2002) postulated this could be the case if salmon from the different rivers might go to different parts of the ocean, or even to the same parts of the ocean at slightly different times or to the same areas but with stays of longer or shorter duration. He suggested that it was difficult to see how findings of common decadal trends of size and condition, but with consistent long-term differences between rivers, as well as coherent annual residual deviations among rivers, would arise or could be maintained if the oceanic stages of 1SW and 2SW salmon from different Scottish rivers followed similar marine migratory routes at similar times. It has been accepted for some time and is consistent with what sparse historical data there was, that European salmon caught in the marine feeding grounds of West Greenland were individuals who returned to spawn after more than one winter at sea (Menzies and Shearer, 1957; Hansen, 1965) with individuals who return after one winter at sea forage mainly in the Norwegian Sea (Jacobsen et al., 2001). This is strongly supported by recent coded wire-tag returns (WGDUHSTI 2007; WKSHINI 2008). However it is not known if the propensity for older maturing salmon originating in Southern European rivers to migrate to the seas of the West Greenland coast is the exception or the rule.

Life history variation, such as the tendency for late maturing, early running fish, or so called ‘Spring salmon’, a characteristic of east coast Scottish rivers (refs), is broadly characteristic of a particular geographical region though within regions there will often be exceptions. For example, in Ireland the predominant phenotype is fish that enter into the rivers in the summer and autumn after spending a single year at sea, yet there are at least six of the larger river systems, which are atypical and like their east coast Scottish counterparts have late maturing, spring running fish. The relative frequencies of life history phenotypes may be influenced by differences in marine environments. However, it is likely that a genetic or heritable basis underpins such life history variation is conditioned via density dependent selection in freshwater, which is itself a function of habitat regulated processes. It has been shown by Stewart et al. (2002) that such differences are heritable and show spatial heterogeneity strongly suggested to be linked to differential expression in different breeding populations within a river stock; the existence of the latter is strongly supported by molecular data (King et al. 2007; Vaha et al. 2011; Dillane et al. *in review*). Gurney et al. (2011) recently concluded that the co-occurrence of multiple sea-age and run time phenotypes of Atlantic salmon within river systems is a stable genetic polymorphism, maintained by some combination of physical separation and asymmetric competition between spawners of different phenotypes or the

riverine stages of their offspring or both. Since grilse and MSW salmon might pursue different marine strategies, it seems very likely that each individual's time-at-sea strategy must be fixed before it emigrates to sea (or at most within a few months of emigration).

2) Main findings from SALSEA-Merge

Understanding of this aspect of the marine ecology of the Atlantic salmon was not specifically advanced. However, the data sets generated when combined with results from future work exploiting the GRAASP to identify the origin of fish, will provide the basis for exploring these issues and advancing understanding.

3) Summary/importance/gaps

It has been demonstrated in the SALSEA-Merge project that the GRAASP tool can identify fish captured at sea with respect to their region or river of origin with great accuracy. It will be possible as the GRAASP undergoes various iterations in its future development (increased baseline resolution and addition of new markers etc – see Final Report) to assign fish collected at sea to reveal much finer levels of sub river structuring. This will be particularly valuable when this can be associated with specific quantitative genetic variation. Future studies will increase in intensity and coverage of marine sampling e.g. plans to genotype archive material from Faroes and West Greenland and to undertake new studies of areas of the Atlantic not previously surveyed e.g. Barents Sea and Irminger Sea. These studies represent the best opportunity to determine for specific river population components when and where life history types diverge in the ocean. An unequivocal demonstration of ocean distribution diverged phenotypes would provide excellent opportunity to make the link between feeding areas, which can be defined oceanographically and whose exact boundaries vary from season to season and from year to year, with temporal trajectories in regional abundances of, for example, sea age of maturity and run time phenotypes. This proffers some possibility for managers to improve stock size predictive capacity and to recognize and respond ecosystem (regime) changes as they occur. Up until now mortality estimates for different sea ages are published on this basis of fairly simple incremental survival models that take little account of population specific distribution and migration patterns (Crozier and Potter, 2000; Friedland et al., 2000). The where-with-all now exists to acquire data to re-formulate life history tables for populations from different regions and rivers with considerable benefits for the forecasting pre-fishery abundance.

Distribution

1) Background

Atlantic salmon smolts leave fresh water and the post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g. Thorpe 1988; Mills 1989). The duration of estuarine residence seems to be relatively brief (Thorstad et al 2007). 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). When they have reached oceanic areas they distribute over large areas of the North Atlantic (Holm et al. 2004). In the marine phase, they feed in surface waters, and mainly occupy the upper 30 m of the water column, but with some occasional dives to larger depths (Holm et al. 2004). At the population level, the distribution at sea was not known before the SALSEA-Merge project started, but fish originating from several rivers have been shown to be present in the same areas (Hansen and Jacobsen 2000; Hansen and Jacobsen 2003). The distribution at sea probably depends on a combination of factors such as food availability, water temperature and currents, as well as on genetic components that govern population specific navigation systems (Hansen and Quinn 1998; Holm et al. 2004; see also Figure 1).

A number of post-smolts have been caught in oceanic areas from the North Sea to the Norwegian Sea during pelagic trawl surveys in the Norwegian Sea in July and August (Holst et al. 1993; Shelton et al. 1997; Holm et al. 2000; Holm et al. 2004), and north of Scotland in May and June (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).

For migratory fishes, such as Atlantic salmon, temporal variation in the utilization of thermal and depth habitats in the marine environment is likely to occur at both broad and fine scales, reflecting ecological and metabolic factors (Hansen and Quinn, 1998; Jonsson *et al.*, 2003; Friedland *et al.*, 2003). Up to the present, much of what is known about the behaviour and life history of salmon at sea has, and continues to rely upon information gathered from commercial catches and research cruises (e.g. SALSEA-Merge program; NASCO, 2008). Research cruises, however, are expensive and limited by the amount of territory that can be covered during a single mission at sea. So recently, more technologically complex methods have begun to come into use, such as earth observation satellites to collect oceanographic data (Holst *et al.*, 2000; Reddin *et al.*, 2000), and data storage tags (DSTs) and acoustic tracking tags to obtain information on salmonid fishes at sea (e.g. Rikardsen *et al.*, 2007). Reddin *et al.* (2004) have shown that DSTs can be particularly useful in collecting data on Atlantic salmon kelts and smolts, even using simple technology that only records temperature and date/time. Additionally, particle tracking models using ocean current fields from ocean model have shown to be useful for estimates of migration pathways and distribution of specific stock groups (Booker et al., 2008; Part 1 in this report). Migratory species are known to change routes in association with changing currents, temperature and salinity distributions (Minns et al. 1995; Ottersen et al. 2004). If post-smolts are forced to swim greater distances in order to discover suitable thermal habitat, a growth effect may be detected.

2) Main findings from SALSEA-Merge

The post smolt migration model together with tag recoveries and genetic stock assignments provided different migration routes for different stock groups. Within SALSEA-Merge the post smolts were found to migrate northwards following the main ocean currents, and the importance of the post smolts temperature and salinity preferences on the distribution was revealed as well. For example, avoidance of coastal water forces the post smolts away from the Norwegian shelf and more into the centre of the Norwegian Sea. Tag recoveries of post smolts showed an active swimming behavior and

the swimming speed was approximately on the same order as the speed of the ocean currents. When reaching the feeding area the post smolts were spread over a large area in the northern Norwegian Sea, but still within Atlantic Water masses. In the feeding area the ratio of overlap in distribution between the different geographical groups from genetic assignment was estimated and fish from Ireland and Scotland dominated over fish from Norway. Changes in migration routes for different years due to changes in the ocean currents (and winds) were found, and this was particularly important for the southern stock group (e.g. Irish fish). Years with weaker southwesterly (or northerly) winds gave a more eastern distribution compared to years with strong westerly winds. In the latter case, the northward migration was faster and consequently; the post smolts reach the feeding area faster. The main distribution of the post smolts were found in water with temperatures between 9-12 °C. It is anticipated that a warmer climate will move this preference area northwards resulting into a longer travelling distance.

3) Summary/importance/gaps

Migration routes may alter because of changes in the ocean currents and winds. Several key regions are identified where shifts in migration may occur resulting into different post smolts distributions. Different stock groups are affected differently because some migration routes may alter more than others. There are several areas that are not covered within the Norwegian Sea the whole time, and some areas have also never been covered, such as south of the Faroese.

Climate

1) Background

Climatic variations play a major role in shaping the marine environment and can influence currents, gyres and sea surface temperatures. Such changes may impact upon salmon directly through altering factors influencing migration routes or indirectly by shifting the distribution, and/or quantity, of food availability at one or several levels in the oceanic food chain. Furthermore, sea temperature may also determine abundance and distribution of potential salmon predators and competitors. Temperature is also a key factor for the physiological metabolism of salmon, and thus affects growth rates. Through altered thermal regimes, climate variability may have a direct affect on the growth rate of many fish species (Reddin et al. 1997; Niva and Jokela 2000; Ottersen et al. 2004), while the survival and growth of Atlantic salmon is also affected via several indirect mechanisms (Ottersen et al. 2004). In addition to alteration of migratory pathways, climatic variability affects the conditions experienced by post-smolts before they have the opportunity to actively pursue a preferential habitat.

The alteration of suitable migratory pathways has been suggested as a factor in the survival of North American post-smolts (Friedland et al. 1999) and should be considered for European stocks, as well. Habitat shifts in response to climatic alterations have already been reported for many species in the North Sea (Perry et al. 2005). The nursery habitat for Atlantic salmon is dynamic and depends integrally on the abundance of primary production to support a prey base. An alteration in suitability

of any of the habitats utilized will affect the population characteristics of a migratory species (Reddin et al. 1997) and may contribute to an alteration of the predator-prey relationship in addition to the direct energetic cost. Thus any disruption or alteration of the migratory/nursery corridor may detrimentally modify the predation pressure experienced by post-smolts in addition to increasing energy expenditure.

Changes in marine environments may change life history of salmon. A changed climate may for example change the timing of smolt migration. There is an apparent optimal sea temperature at post-smolt entry. If temperatures in the freshwater and marine environments are not synchronised, this may affect the mortality of post-smolts. For example, if temperature increases in freshwater, the smolts may be triggered to migrate to sea earlier. But if the sea temperature has not changed, or has decreased, this would result in the smolts moving into an environment that is not optimal for them.

A changed marine climate may also affect growth rate and thus sea age at maturity. Hutchings & Jones (1998) found a positive correlation among population association between sea-age at maturity and growth rate at sea for Atlantic salmon, as was also observed by Jonsson *et al.* (2002). Thus a faster growth in the marine environment may produce salmon with younger sea age.

The recent changes in the NAO index (a measure of the difference in atmospheric pressure between a northern and southern area of the North Atlantic) to extreme positive states has led to increased interest in how such changes impact upon growth and survival in Atlantic salmon. It has been shown that a strong positive correlation exists between the NAO and indices of salmon. The NAO can influence temperature, wind strength, salinity and wave height, all factors that could have effects on recruitment through a range of mechanisms at different stages of the salmon's life cycle (including freshwater effects).

2) Main findings from SALSEA-Merge

The SALSEA-Merge migration model showed how the changes in the ocean current due to wind changes alter the migration routes of post smolt. However, this effect the different stock groups differently. Strong southwesterly winds (high NAO index) force a more eastern migration route within the Norwegian Sea while weak southwesterly (or northerly) winds (low NAO index) results in a more western migration route. The latter case also opens up a migration route toward Iceland for the southern stock group. Thus, the overlap in distribution of different stock groups changes over time due to changes in the climate that affect the migration routes. Changes in climate not only affect the ocean currents but also the environment. First, the temperature at the post smolt entry was found to vary with years. Under a warmer climate this will trigger an earlier smolt migration that could result into a mismatch between the post smolt distribution and the environment. Also, the prediction of a future climate is area dependent meaning that different stock groups are affected differently. Second, since the post smolts have some temperature preference a warmer climate will move the temperature preference area northwards; resulting into a longer travelling distance for the post smolts.

3) Summary/importance/gaps

Climate variability affects the migration routes through changes in the ocean currents and different stock groups are differently affected. A warmer climate affects the survival of the post smolts through several processes. The post smolts may migrate a longer distance to stay in the preferred temperature range, but also an earlier smolt migration date may alter the present life cycle. There are still large uncertainties in how the future global climate change will affect the regional climate and the ocean currents; factors that are important for the survival of the post smolts.

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