



SID 5 Research Project Final Report

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Executive Summary

7. The executive summary must not exceed 2 sides in total of A4 and should be understandable to the intelligent non-scientist. It should cover the main objectives, methods and findings of the research, together with any other significant events and options for new work.

Populations of Atlantic salmon have declined throughout the species' range. The primary causes may vary among populations, but it appears that there has been a widespread decrease in survival during the marine phase, associated with reduced growth rates. It is therefore important for efforts to conserve salmon populations to understand how changes in oceanic conditions might affect growth and survival.

The aim of this research was to develop a numerical model for investigating potential changes in the growth and survival of Atlantic salmon during the marine phase arising from changes in smolt condition or oceanic conditions. A numerical model was designed to calculate growth and survival resulting from spatial and temporal patterns of physical oceanographic conditions, specifically ocean currents, sea surface temperature and prey availability.

We developed a physiologically and physically-based numerical modelling approach to investigate the effects of changing oceanographic conditions on the growth and survival of migrating Atlantic salmon. The model consisted of a set of equations that was used to describe adult salmon growth and survival in the ocean. An individual-based bioenergetic approach was taken, which seeks to assess survival and growth by quantifying the balance between energy gained from feeding and energy lost through maintenance, activity, digestion, food capture, growth, nitrogenous excretion and faeces. No field or laboratory experiments were carried as part of this project. Therefore only existing information were used to develop and test the bioenergetic model. Where possible we used published information on wild adult Atlantic salmon for representation of adult salmon physiology. The individual-based Lagrangian model was then deployed within an Eulerian marine environment to assess the relative importance of both future and past inter-annual variations in temperature, prey availability and surface currents on the growth of Atlantic salmon. Data from an ocean circulation model, a coupled ocean-ecosystem model and from measured climatologies were used to represent conditions in the marine environment.

A suite of sensitivity experiments were conducted to investigate the robustness of the modelled mechanisms for controlling salmon growth and survival. These experiments took the form of both spatial and non-spatial experiments. The sensitivity of salmon length predicted by the bioenergetic model to changes in the model physiological parameters was tested by varying parameters with combinations of water temperature and swimming speed. Growth was very sensitive to certain parameters of the main bioenergetic functions, i.e. those for maximum daily consumption, respiration and allocation of assimilated energy. Other parameters had moderate effects, whereas parameters associated with prey encounter rate and ingestion had little influence on growth. Some of the sensitive parameters had a reliable empirical

provenance, whereas appropriate values for others were less certain, owing to the species or circumstances from which they were derived.

The model was used to assess how changes in smolt length, smolt year, date of entry to the ocean, swimming speed, location of feeding ground and home-river can affect growth and survival of Atlantic salmon. Our results indicated that salmon that left their home-rivers earlier in the year or as larger smolts were likely to return as larger adults. Results also indicated that salmon travelling towards more northerly feeding grounds did not grow as much as those travelling on shorter migrations. Overall, these numerical experiments suggested that our ability to model that affects of changing oceanographic conditions on salmon growth and survival is limited more by our lack of knowledge on salmon behaviour in the open ocean rather than a lack of knowledge on the physiological processes controlling growth.

Information on the possible migration routes of migrating salmon were obtained using data on the recapture positions of salmon that were tagged in their home-rivers as well as data on the position of salmon caught in fishing trawls. The impact of ocean surface current patterns on the speed and timing of salmon migration routes were investigated. For example, trajectories of tagged salmon that left the west coast of Ireland in 1996 and 1997 and were recaptured during the first two months at sea were simulated using rheotaxis as a direction-finding mechanism and a constant swimming speed of 0.2 m s^{-1} . Simulated trajectories were significantly affected by the way in which surface currents were represented. When a mixed layer depth was used in the calculation of currents, 78% of the simulated trajectories passed within 40 km of the observed recapture location. This work indicated that rheotaxis is one possible direction-finding mechanism for migrating Atlantic salmon during the first two months at sea.

Data on the positions of tagged salmon during their first winter at sea were also used to test the model. Results showed that it is unlikely that these salmon would have obtained their recaptured locations by swimming in random directions. Therefore there must be some mechanism, or combination of mechanisms, that act to influence the trajectories of migrating Atlantic salmon. Comparisons of the positions simulated using different direction finding mechanisms showed that different mechanisms could result in similar trajectories and similar areas of the ocean being occupied. It is possible that in reality combinations of mechanisms are being employed. For example, salmon may be heading for cooler waters and using rheotaxis at the same time. Several mechanisms may have been responsible for creating the patterns of migration towards the Norwegian Sea that have been inferred from trawl data. These include rheotaxis, thermotaxis and prey searching.

We tested predictions of growth calculated by the model using a limited number of observations of lengths of salmon that were tagged in their home-rivers and subsequently recaptured after several months at sea in December. Further data were available for salmon that were captured on return to their home-rivers. These comparisons showed good correspondence between observed lengths and those calculated by the model. For example, observations from the Rivers Wear, Coquet, Dee and Frome suggest that typical one sea-winter fish returned to their home-rivers in mid-August after having grown to sizes ranging from 0.5 to 0.8 m with an average size of 0.65 m. When forced to follow a representative set route, simulated salmon leaving these rivers grew to lengths of 0.60, 0.60, 0.59 and 0.66 m respectively.

Different sources of information were used to represent the spatial and temporal patterns of oceanic conditions experienced by the salmon. We first investigated the relative importance of inter-annual variations in prey availability, sea surface temperature and surface currents on salmon growth using the most accurate information available for 1993–1999. When the salmon were given final destinations that represented feeding grounds to swim towards and did not alter their migration trajectories according to local conditions, inter-annual changes in currents were capable of advecting them long distances and therefore affecting growth rates through changes in temperature and prey availability. When salmon followed these fixed trajectories, inter-annual variations in prey availability and temperature had far less of an influence on length, in comparison with the position of the home-river and the position of the final destination. Under this migration scenario, changes in growth between years could be dominated by changes in temperature rather than prey availability, although changes in prey availability did influence salmon growth in high latitudes. Salmon trajectories that might have resulted from reactions to local conditions were also simulated. When thermotaxis was implemented as an example of this type of behaviour, inter-annual changes in currents or prey had less influence on growth than inter-annual variations in temperature.

We then used longer-term, but perhaps less reliable, data on changes in temperature and prey availability to investigate longer-term trends over the period 1970 to 2001. Results showed that, using thermotaxis, inter-annual changes in temperature patterns could lead to changes in salmon growth and survival. Under this migration scenario, there was little variation in growth of salmon leaving British rivers during the 1970's. Greater variations in predicted lengths were calculated for the 1980's and 1990's. There was a marked reduction in hindcasted salmon length in smolt years 1982, 1986 and 1993. The North Atlantic

Oscillation for these periods was mainly positive, indicating that changes in oceanographic conditions may have predictable impacts on salmon growth and survival. These were smolt years that coincided with predominantly positive North Atlantic Oscillation (NAO) periods. The NAO is a major feature that affects oceanographic conditions, being the major contributor to inter-annual and decadal variations of climate in the North Atlantic Ocean. In particular, it influences the patterns of sea surface temperature and surface currents, which in turn affect the distribution of salmon prey.

The model was then used to predict the effects of inter-decadal variations in future sea surface temperature on calculated lengths, depending on variations in prey availability and regardless of changes in local currents, when the simulated salmon followed the same fixed trajectories. The bioenergetic model, together with future predictions of sea surface temperature, was used to simulate growth of salmon over the period 1990–2100 under one scenario for future climate change (i.e. observed anthropogenic emissions to 1990 and a 'business as usual' scenario thereafter). Given fixed trajectories and steady swimming speeds, increases in temperature were predicted to lead to increased growth, as the salmon experienced warmer temperatures that created more favourable conditions for growth regardless of prey availability. These results suggest that, if all other factors are equal and salmon are following set routes, they will not be adversely affected by climate change driven future increases in sea surface temperature. The results suggested that, given this modelled behaviour, the adverse effects of climate change could be reduced prey availability or a change in current patterns. A different result was obtained when thermotaxis was used to simulate the type of behaviour that might result when the salmon attempt to locate and remain within particular conditions. Under this particular migration scenario, increases in temperature led to a slight decrease in growth. Many of the simulated salmon were able to remain within the specified temperature range by seeking similar conditions elsewhere in the ocean. This suggests that, during their oceanic phase, salmon may be capable of adapting to future climate change provided that their migration routes are not inherited and guided by other cues (e.g. celestial or wave patterns). However, our ability to predict the effects of climate change on salmon populations is limited by a lack of knowledge about migration behaviour, which in turn is due to the paucity of observations of salmon movements and growth in the open ocean.

Salmon populations could be effected by climate change during their freshwater as well as their marine phases. The model that was developed for this project only considered the marine phase of the salmon life-cycle. Future work could be developed to link the marine and freshwater life-stages. This would allow better understanding of the combined effects of climate change on both the freshwater and oceanic phases on salmon whole life-history strategies.

Project Report to Defra

8. As a guide this report should be no longer than 20 sides of A4. This report is to provide Defra with details of the outputs of the research project for internal purposes; to meet the terms of the contract; and to allow Defra to publish details of the outputs to meet Environmental Information Regulation or Freedom of Information obligations. This short report to Defra does not preclude contractors from also seeking to publish a full, formal scientific report/paper in an appropriate scientific or other journal/publication. Indeed, Defra actively encourages such publications as part of the contract terms. The report to Defra should include:
- the scientific objectives as set out in the contract;
 - the extent to which the objectives set out in the contract have been met;
 - details of methods used and the results obtained, including statistical analysis (if appropriate);
 - a discussion of the results and their reliability;
 - the main implications of the findings;
 - possible future work; and
 - any action resulting from the research (e.g. IP, Knowledge Transfer).

Modelling the bioenergetics of salmon migration

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A more detailed record of the methodology, results and findings of this project are given in:
Booker, D.J., Smith, I.P., Wells, N.C., (2006). Modelling the bioenergetics of Salmon migration. Final report.
DEFRA Project number SF0237. CEH project number C02029. August 2006, pp194.

Background

Populations of Atlantic salmon have declined throughout the species' range. The primary causes may vary among populations, but it appears that there has been a widespread decrease in survival during the marine phase, associated with reduced growth rates. It is therefore important for efforts to conserve salmon populations to understand how changes in oceanic conditions might affect growth and survival.

Project aim

The aim of this research was to develop a numerical model for investigating potential changes in the growth and survival of Atlantic salmon during the marine phase arising from changes in smolt condition or oceanic conditions. A numerical model was designed to calculate growth and survival resulting from physical oceanographic conditions, specifically ocean currents, sea surface temperature and prey availability.

We developed a physiologically and physically-based numerical modelling approach to investigate the effects of changing oceanographic conditions on the growth and survival of migrating Atlantic salmon. An individual-based (*sensu* Grimm, 1999) bioenergetic approach was taken, which seeks to assess survival and growth by quantifying the balance between energy gained from feeding and energy lost through maintenance, activity, digestion, food capture, growth, nitrogenous excretion and faeces. The individual-based Lagrangian model was then deployed within an Eulerian marine environment to assess the relative importance of both future and past inter-annual variations in temperature, prey availability and surface currents on the growth of Atlantic salmon.

Progress on objectives

Objective 1, Bioenergetic model development

A bioenergetic model was developed to simulate the growth and survival of individual adult salmon in the ocean. This model consisted of a set of equations that was used to describe salmon growth and survival. The model estimated the energy balance of individual salmon by calculating the amount of energy gained when feeding in comparison to energy lost in respiration, digestive and excretory processes. The model was developed using published information on salmonid physiology. Where possible we used published information on wild adult Atlantic salmon for improved representation of adult salmon physiology. This led to the recalculation of some model parameters and algorithms that had previously been calculated for juveniles in freshwater.

Objective 2, Representations of surface current patterns

Representations of surface currents were gained from the Ocean Circulation and Climate Advanced Model (OCCAM) general circulation model forced by realistic winds (Webb et al., 2000). We calculated surface current representations at a 0.25° resolution on a monthly time-step covering the period 1993–1999 (Figure 1). A comparison of the simulated currents with World Ocean Circulation Experiment (WOCE) (Jakobsen et al., 2003) data derived from drifting buoys showed that the model currents reproduce many detailed circulation features of the surface circulation of the North Atlantic ocean (Figure 2). In order to reproduce the observed drifter trajectories the momentum in the model was mixed over a climatological mixed layer depth. Comparison of Eulerian velocities showed generally good correspondence between the direction of the drifters and the direction of the model currents, although the speed of the model currents was generally slightly underestimated. Various statistical methods were used to explore the simulated current data and test the correspondence between the observed and calculated currents. These included major axis regressions, randomized block analysis of variance (ANOVA) and Tukey's multiple comparison test.

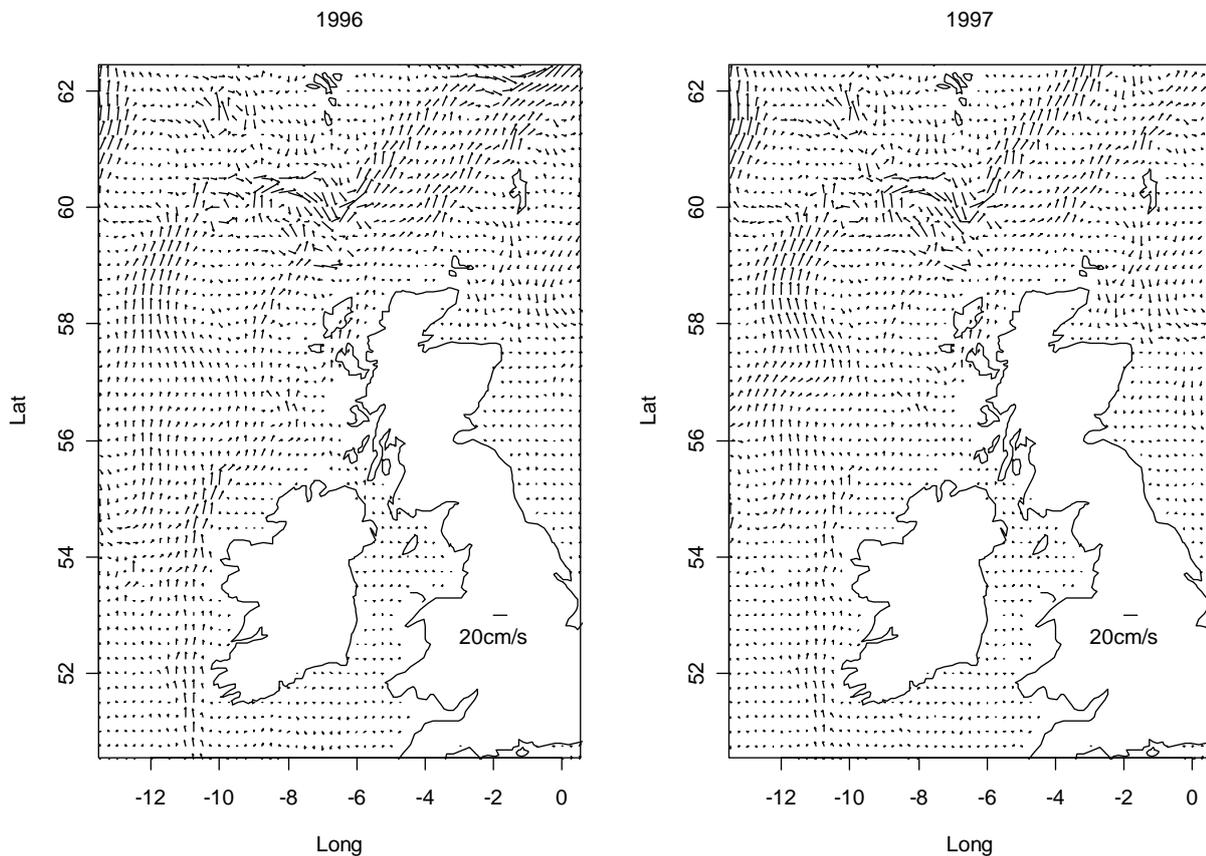


Figure 1. Hindcasted near-surface velocity for 16th May 1996 and 1997.

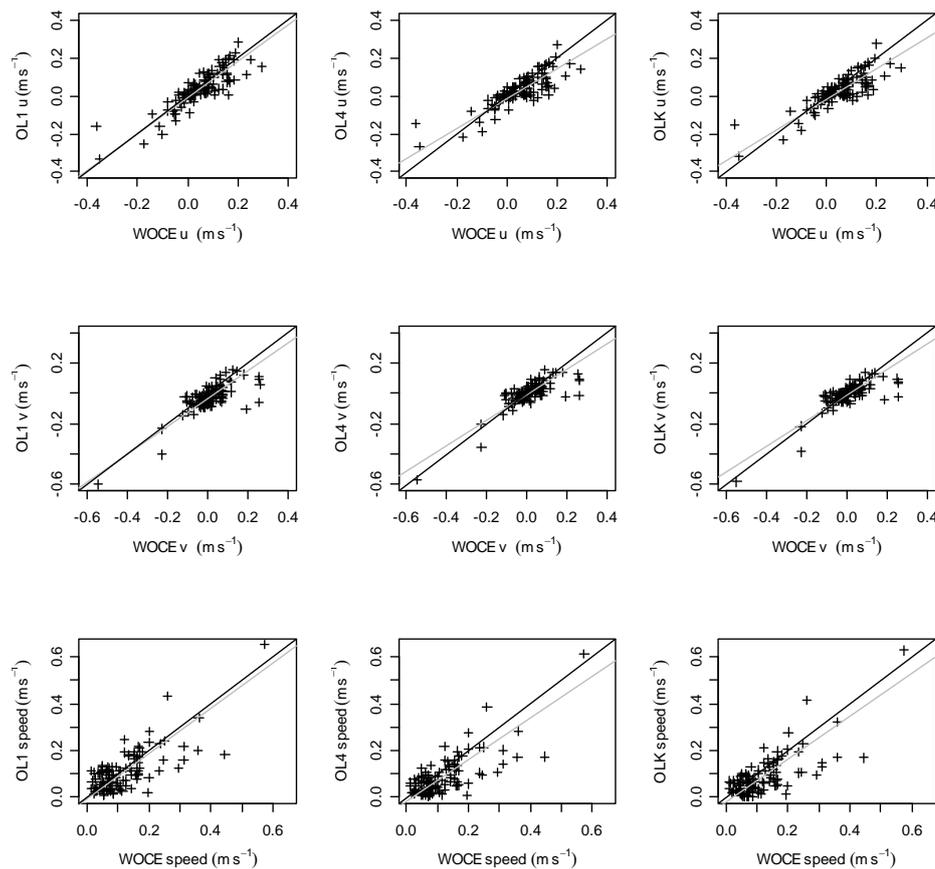


Figure 2. Comparison of Eulerian mean currents 1993–1998 for 5° boxes from WOCE drifters and OCCAM. Black line indicates observed = calculated. Grey line indicates major axis regression line.

Objective 3 Climate change scenarios

Sea surface temperature data were obtained from several different sources. We obtained high-resolution data on measured sea surface temperatures from both the HadSST and the Reynolds climatology data sets for the period 1993–1999. We also obtained representations of sea surface temperatures covering the period 1970–2002 from a Met Office coupled physical-biogeochemical model. Further data from the same model were obtained that represented the period 1990–2100 and included the effects of a future climate change scenario. The particular future scenario that we used employed observed anthropogenic emissions to 1990 and the IS92a scenario thereafter (Johns et al., 2003). The IS92a scenario is a ‘business as usual’ scenario, which assumes mid-range economic growth but no measures to reduce greenhouse-gas emissions and in which the atmospheric concentration of carbon dioxide more than doubles over the course of the 21st century.

Objective 4, Salmon prey abundance

Analysis of stomach contents indicates that salmon can prey on a wide variety of invertebrates and fish during their marine phase. Zooplankton biomass/abundance survey results and catch statistics for small pelagic fisheries are available; however, these are too sparse in time and space to construct a prey distribution map at the scales required for bioenergetic modelling. We had originally planned to produce scenarios of the spatial distribution of salmon prey availability using expert opinion. During the course of the project we improved upon this methodology. The abundance of potential salmon prey items were calculated from the output of a coupled physical-biogeochemical model. The Hadley Centre Ocean Carbon Cycle (HadOCC) model is a coupled physical-biogeochemical model of the ocean carbon cycle (Palmer and Totterdell 2001). This provided a representation of patterns of zooplankton biomass (Figure 3) and zooplankton biomass lost to higher predators. Initial validation of the modelled data showed good correspondence between the converted HadOCC output and measured zooplankton abundance at the L4 plankton monitoring station (Plymouth) and on the Svinøy transect (Norway) (Figure 4). Given a lack of empirical data, the prey size/species spectrum was represented by seven categories for simplicity. The proportion of total biomass represented by each prey category was then applied to the total biomass to estimate biomass by category. Average individual weights obtained from published weight-length relationships were used to calculate numerical abundance of each prey category from its biomass. Published values of: length to weight ratio; energy density; and dry weight to wet weight ratio were then used to calculate the energetic gain that a salmon would obtain from consuming a single prey item from each category.

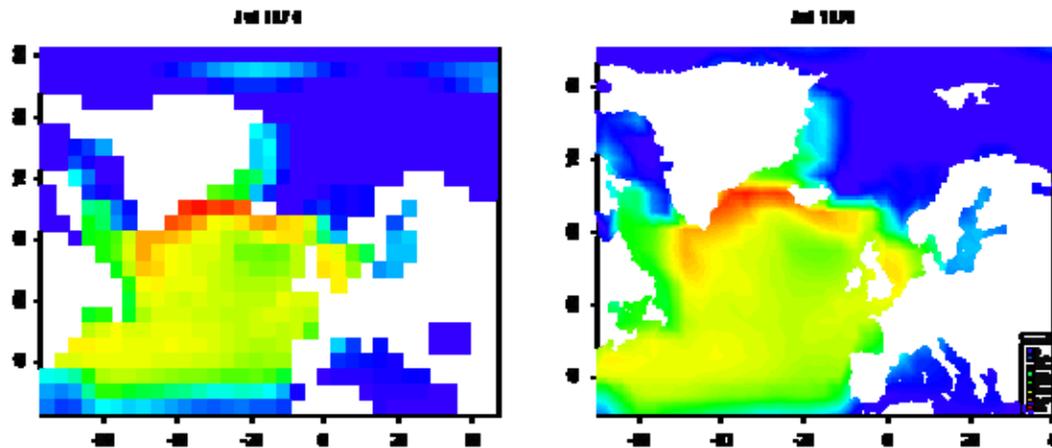


Figure 3. Zooplankton concentration maps. Left: HadOCC (data obtained from Ian Totterdell, Met Office). Right: interpolated onto SalarSim landmask.

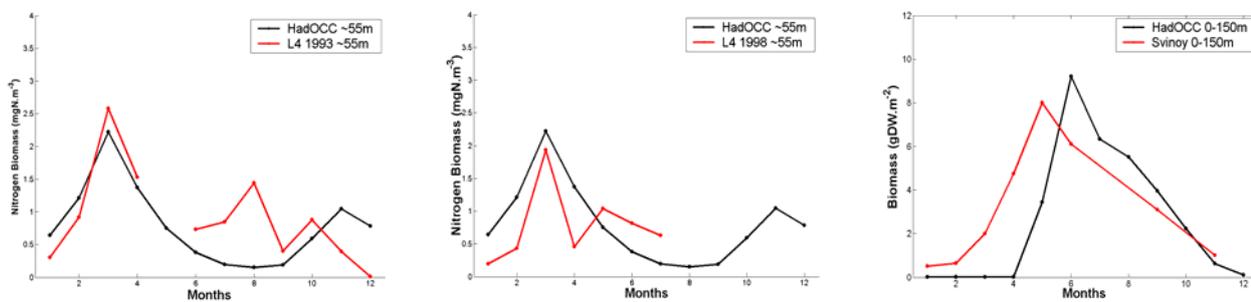


Figure 4. Monthly means of Zooplankton Biomass from the HadOCC model and Observations.

Objective 5, Spatial bioenergetic model

The surface currents, sea surface temperature and prey abundance representations were transferred onto a latitude-longitude grid. This grid included a land mask which was used to represent the position of coasts. Salmon are primarily visual feeders, therefore a day length algorithm was incorporated into the model. This allowed calculation of the day light hours at any point in North Atlantic. The total coverage of the model was: 35°N–85°N and 70°W–40°E in increments of 0.25°. We used monthly mean data in all cases and then employed spatial and temporal interpolation schemes to estimate conditions on any day at any location within the model domain.

Objective 6, Modelling migratory routes, growth and survival

The salmon physiology algorithms were combined with the spatial representations to allow individually-based modelling of migration routes, growth and survival. Several scenarios describing direction finding mechanisms and swimming speeds were incorporated into the model. Direction finding mechanisms included swimming towards a final destination, searching for specified temperature conditions and searching for areas of high prey abundance. The model also allowed calculation of the optimal swimming speed. This is defined as the most favourable swimming speed in terms of energetic trade-off.

Objective 7, Model testing

No field or laboratory experiments were carried as part of this project. Therefore we used only existing information to develop and test the bioenergetic model. We tested the models ability to predict migration trajectories using observed data on salmon. We obtained information on the possible migration routes of migrating salmon using data on the recapture positions of salmon that were tagged in their home-rivers as well as data on the position of salmon caught in fishing trawls (Holst et al., 2000). We used the representations of surface currents to investigate the impact of ocean surface current patterns on the speed and timing of salmon migration routes. For example, trajectories of tagged salmon that left the west coast of Ireland in 1996 and 1997 and were recaptured during the first two months at sea were simulated using rheotaxis as a direction-finding mechanism and a constant swimming speed of 0.2 m s⁻¹. Simulated trajectories were significantly affected by the way in which surface currents were represented. When the mixed layer depth (OLK) was used in the calculation of currents, 78% of the simulated trajectories passed within 40 km of the observed recapture location (Figure 5). This work indicated that

rheotaxis is one possible direction-finding mechanism for migrating Atlantic salmon during the first two months at sea.

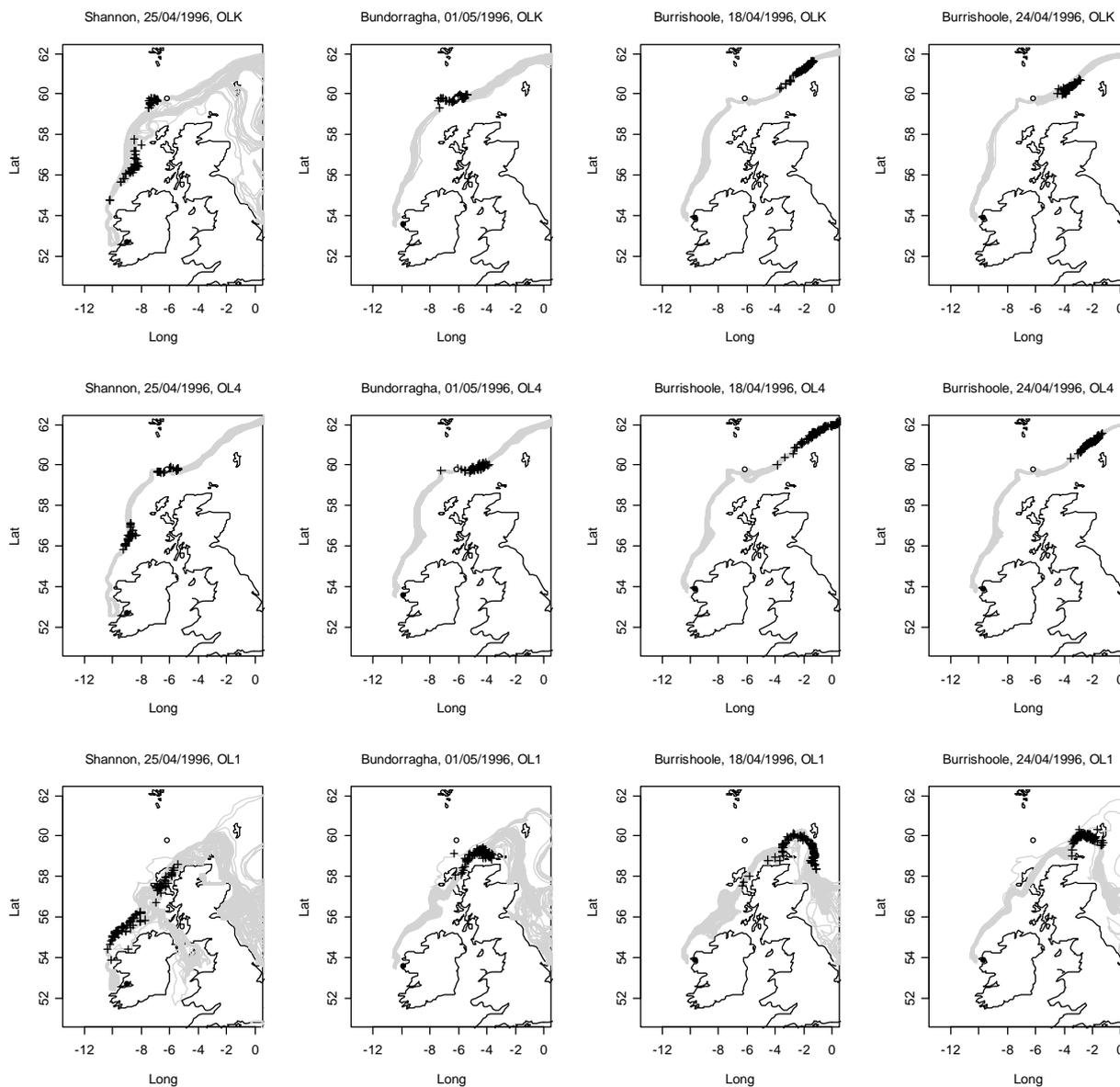


Figure 5. Simulated trajectories (grey lines, $n=100$) of recaptured tagged salmon swimming at 0.2 m s^{-1} using rheotaxis to follow local currents in 1996. Crosses indicate simulated position on date of recapture. Closed circles indicate home river. Open circles indicate position of actual recapture (after data from Holst et al. 2000). Titles show name of home river, date of release and hindcasted current representation used in calculation. OL1 = OCCAM layer 1, OL4 = OCCAM layers 1–4, OLK = mixed layer depth calculation.

Data on the positions of tagged salmon during their first winter at sea (personal communication. Ian Russell, CEFAS) were also used to test the model. Results showed that it is unlikely that the wire tagged salmon would have obtained their recaptured locations by swimming in random directions. Therefore there must be some mechanism, or combination of mechanisms, that act to influence the trajectories of migrating Atlantic salmon. Comparisons of the positions simulated using different direction finding mechanisms showed that different mechanisms could result in similar trajectories and similar areas of the ocean being occupied. It is possible that in reality combinations of mechanisms are being employed. For example, salmon may be heading for cooler waters and using rheotaxis at the same time. Several mechanisms may have been responsible for creating the patterns of migration towards the Norwegian Sea that have been inferred from trawl data (Holst et al., 2000). These include rheotaxis, thermotaxis (e.g. Figure 6) and prey searching.

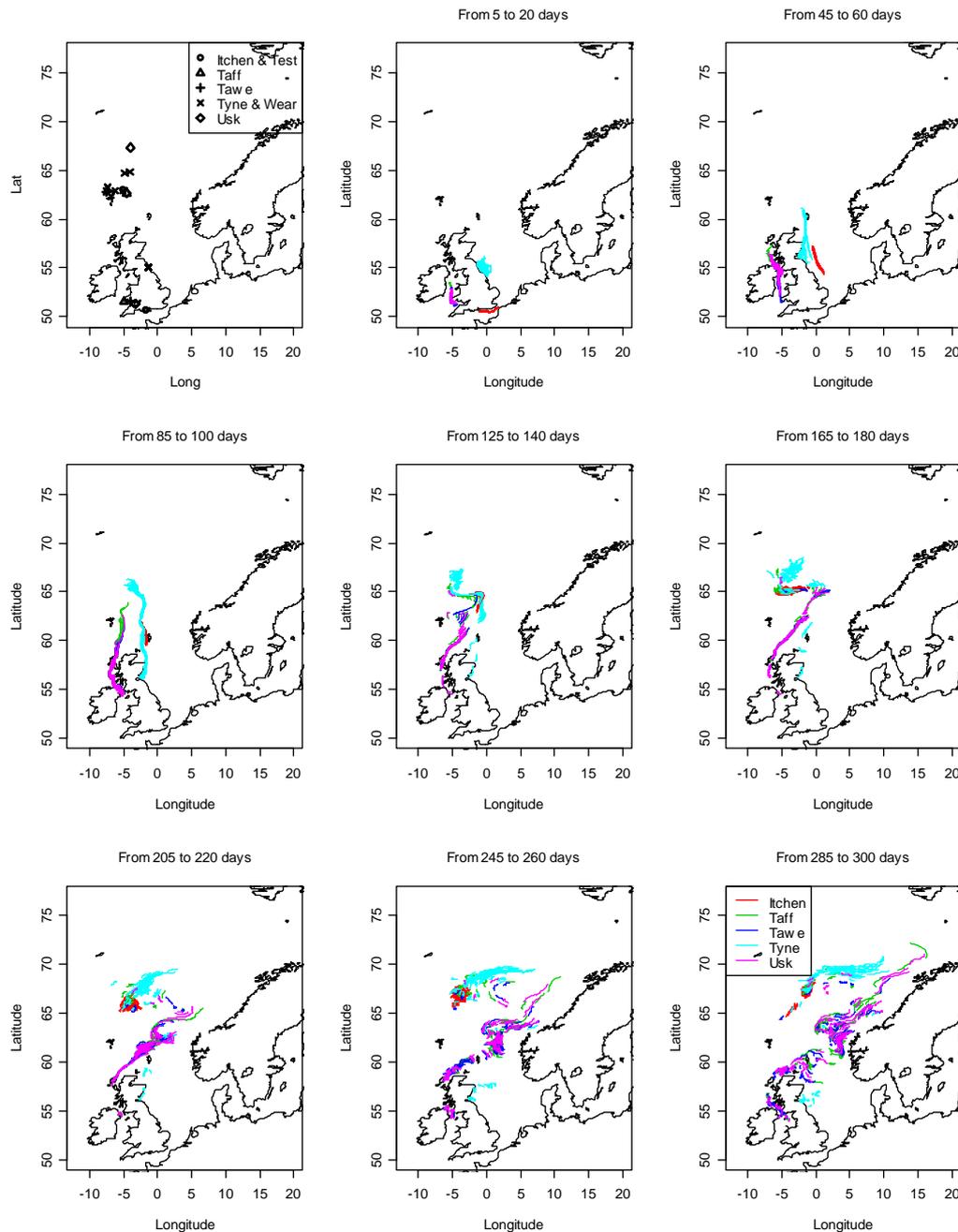


Figure 6. Recapture positions of tagged salmon and simulated positions of 100 salmon from each river using thermotaxis between 4–9 °C at a constant swimming speed of 0.2 m s⁻¹ for 100 days followed by swimming at the optimal swimming speed.

We also tested predictions of growth calculated by the model using observed data on salmon lengths. Some data were available for salmon that were tagged in their home-rivers and subsequently recaptured after several months at sea in December. Further data were available for salmon that were captured on return to their home-rivers. Observed lengths of tagged salmon that were caught off the north east coast of the Faroes were compared with lengths calculated by the model. Lengths of the tagged and recaptured salmon caught in December were in the range 0.40–0.47 m. Calculated lengths in mid-December were in the range 0.35–0.43 m. Calculated lengths therefore did overlap with the observed data, however, on average the calculated lengths did underestimate lengths in comparison with the observations. This test of the model was undertaken using an observed data set with a very small sample size ($n = 9$). The observed data show that there was considerable variation in sizes of the recaptured salmon. This was even the case for salmon caught in the same month and in the same position. Furthermore, the lengths of the two salmon that were caught in March were 0.43 and 0.45 m. Calculated lengths for the corresponding number of days at sea were in the range 0.42 to 0.47 m. It would therefore appear that calculated lengths corresponded well with observed lengths for these salmon. It was therefore concluded that this model scenario reproduced observations of salmon length given uncertainty in the estimate of the length distribution of the true population. Larger data sets on the condition of salmon at sea are required in order to more fully test this type of model.

Observations from the Rivers Wear (and Coquet), Dee and Frome suggest that typical 1SW fish returned to their home-rivers in mid-August after having grown to sizes ranging from 0.5 to 0.8 m with an average size of 0.65 m. These data were obtained through personal communication with Ian Russell (CEFAS), Ian Davidson (EA) and Anton Ibbotson (CEH) respectively. The model was run using three different direction finding mechanisms, and calculated lengths were compared with observed lengths. When forced to swim toward a representative final destination simulated salmon leaving the rivers Wear, Coquet, Dee and Frome grew to lengths of 0.54, 0.59, 0.59 and 0.72 m respectively. When forced to follow a set route, simulated salmon leaving the rivers Wear, Coquet, Dee and Frome grew to lengths of 0.60, 0.60, 0.59 and 0.66 m respectively. Calculated lengths for both sets of simulations overlapped with the observed range of lengths.

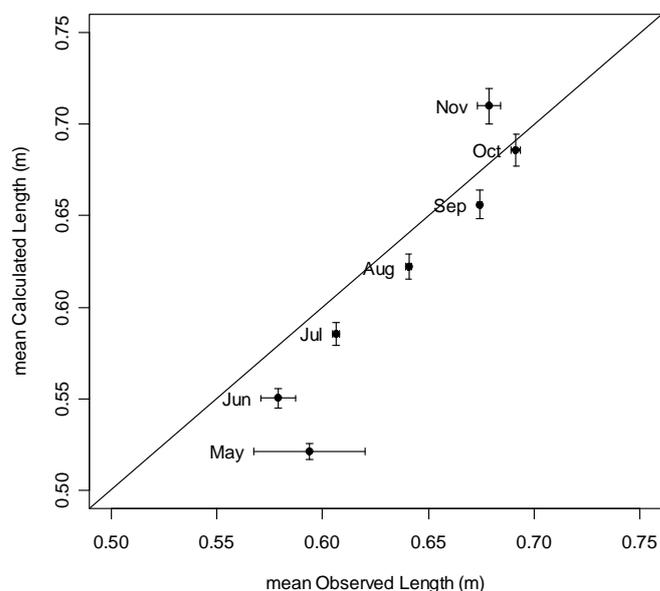


Figure 7. Observed (using thermotaxis 4 to 9 °C) versus calculated mean lengths of one sea winter salmon for the River Dee. Bars indicate 95% confidence interval for the mean.

Variations among individual salmon were included in the model when a thermotaxis scenario was used as a direction finding mechanism. This meant that the model generated a distribution of lengths, which could be compared statistically with the observed data. Using thermotaxis, the model replicated observed seasonal patterns of mean length of grilse for the River Dee (Figure 7). The distribution of calculated lengths was narrower than the observed data and the model slightly underestimated the mean observed lengths. Comparisons between observed and calculated lengths were hampered by several difficulties. The model was able to predict death of salmon caused by starvation. In reality, the salmon may die because of a variety of reasons including starvation, disease and predation. Predation may be size dependent (i.e. smaller salmon may be more vulnerable to being preyed upon). This may partly explain why calculated lengths were smaller than the observed data.

Objective 8, Sensitivity analysis

No field or laboratory experiments were carried as part of this project. Therefore we used only existing information to develop and test the bioenergetic model. There is a considerable body of literature on salmon growth rates in relation to temperature and ration, including some work on the effects of swimming speed. However, there is a lack of empirical data for combinations of values of explanatory variables. We tested the sensitivity of predictions of length to changes to the bioenergetic model parameters and changes in the spatial modelling options.

We conducted a suite of sensitivity experiments to investigate the robustness of the modelled mechanisms for controlling salmon growth and survival. The sensitivity of salmon length predicted by the bioenergetic model to changes in the model physiological parameters was tested by varying parameters individually with combinations of water temperature and swimming speed. Modelled growth varied with water temperature and swimming speed in the manner expected from empirical studies, but was less than that achieved by wild post-smolt salmon. Growth was very sensitive to certain parameters of the main bioenergetic functions, i.e. those for maximum daily consumption, respiration (e.g. Figure 8) and allocation of assimilated energy. Other parameters had moderate effects, whereas parameters associated with prey encounter rate and ingestion had little influence on growth, given the defined prey availability. Some of the sensitive parameters had a reliable empirical provenance, whereas appropriate values for others were less certain, owing to the species or circumstances from which they were derived.

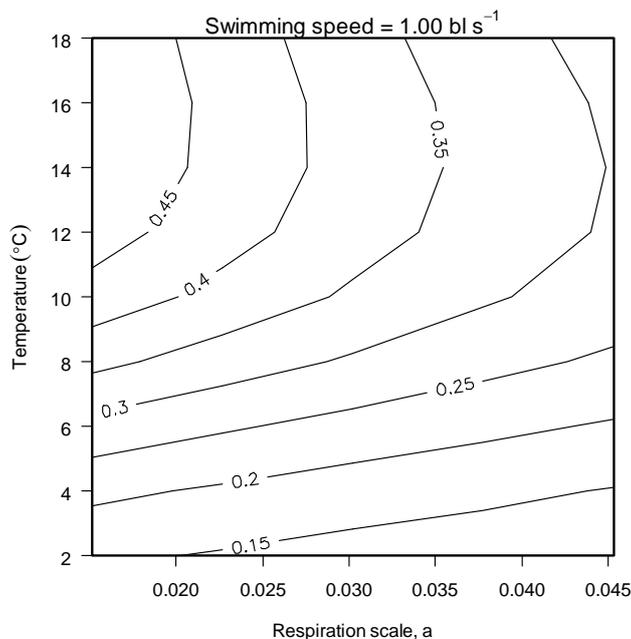


Figure 8. Final salmon length (m) as a function of sea surface temperature and value of the respiration scale ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), at a swimming speed of 1 bl s^{-1} .

Further information that could be used to test the model could be obtained by growth trials in seawater tanks. We outlined a cost-effective protocol to validate this aspect of the bioenergetic model. Facilities in which salmon growth trials could be carried out are listed in the full report. See section of future work below for further details.

Spatially explicit sensitivity tests were used to investigate the spatial aspects of the bioenergetic model. The model was used to assess how changes in smolt length, smolt year, date of entry to the ocean, swimming speed, location of feeding ground and home-river can affect growth and survival of Atlantic salmon (e.g. Figure 9). Our results indicated that salmon that left their home-rivers earlier in the year or as larger smolts were likely to return as larger adults. Results also indicated that salmon travelling towards more northerly feeding grounds did not grow as much as those travelling on shorter migrations. Results also showed that several of the model parameters did not significantly affect the model results. Overall, these sensitivity experiments suggested that our ability to model that affects of changing oceanographic conditions on salmon growth and survival are limited more by our lack of knowledge on salmon behaviour in the open ocean rather than a lack of knowledge on the physiological processes controlling growth.

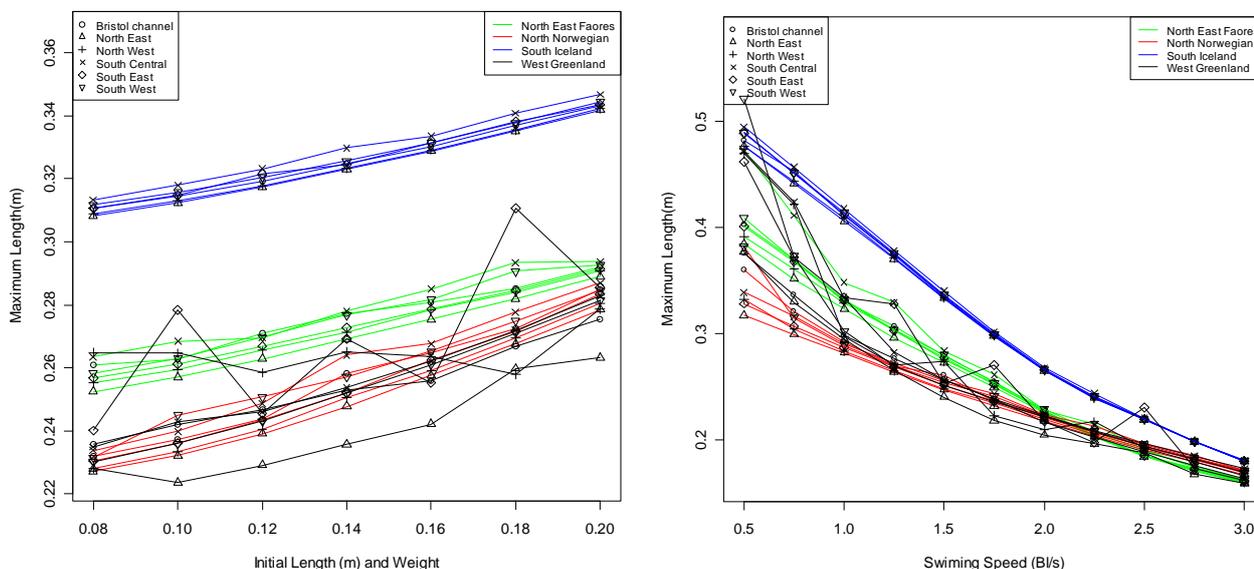


Figure 9. Affect of initial size when using constant swimming at 1.6 l s^{-1} (left) and swimming speed (right) on maximum length.

Objective 9, Implications of the findings and policy recommendations

The model was used to assess the dependence of calculated lengths on inter-annual changes in prey and SST regimes, but regardless of local currents. The method we used was to simulate growth and survival of salmon from seven representative regions of England, Wales and Scotland towards one of four potential feeding grounds in the North Atlantic. Analysis of the variance in calculated length for the period 1970–2001 showed that if all post-smolt salmon were to undertake the same journeys year after year they would be affected by inter-annual changes in temperature or prey in different ways (Figure 10). Inter-annual variations in prey had little effect on the results, except for journeys to the North Norwegian Sea. This was because, for the other destinations, there was sufficient prey availability to reach maximum consumption regardless of inter-annual variations in prey. In all cases most inter-annual differences in lengths were caused when SST and prey were varied together. This indicates that, for this migration scenario, changes in SST were not counteracted by changes in prey availability. Statistical analysis using ANOVA showed that inter-annual changes in SST and prey (together) did have a statistically significant affect on the length of the salmon. However, the strength of this influence was not as significant as that of the location of the home-river or the location of the feeding ground.

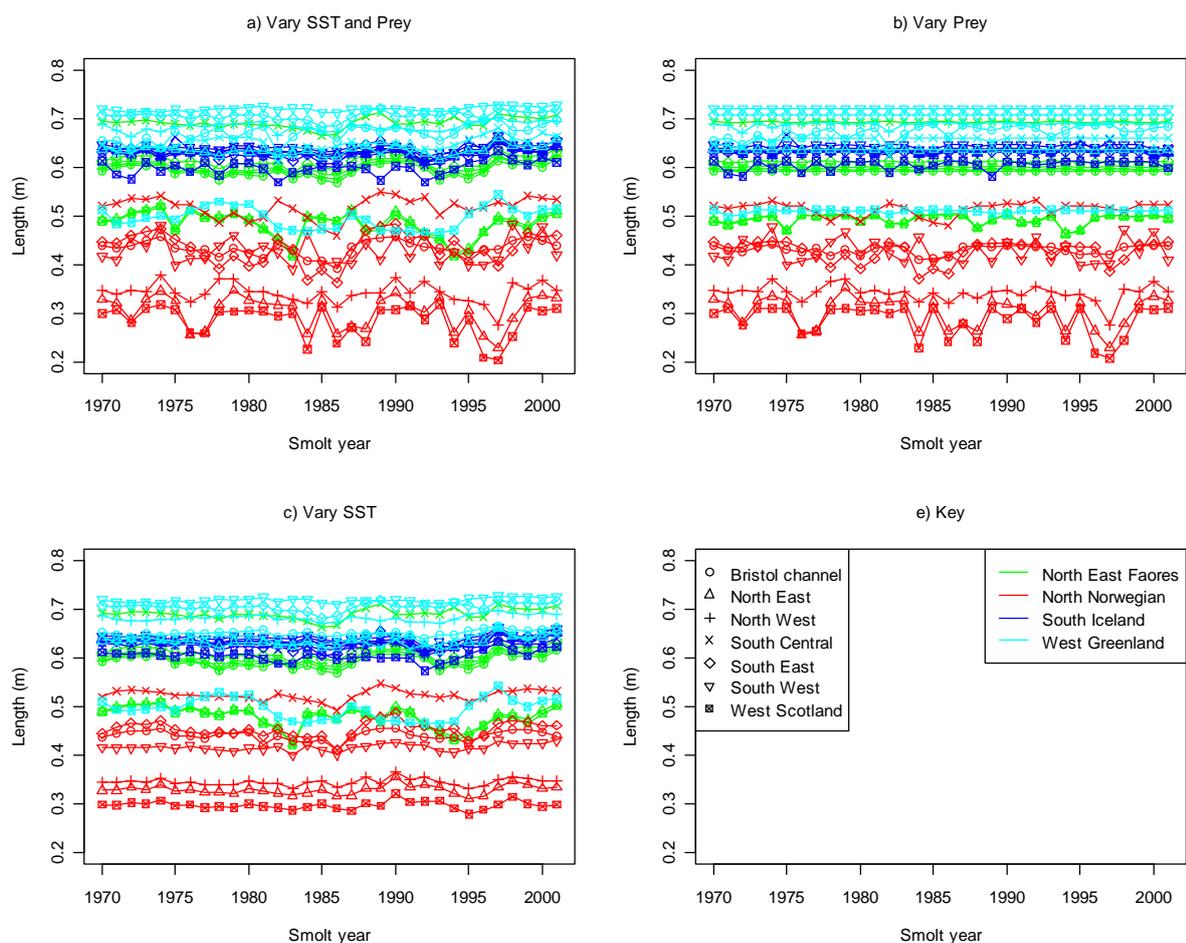


Figure 10. Calculated lengths on the 15th of August for 28 fixed journeys given a) SST and prey from 1970 to 2001 b) prey from 1970 to 2001 SST from 1970–1971 and c) SST from 1970 to 2001 and prey from 1970–1971. All currents set using 1993–1994.

When thermotaxis was implemented as a direction finding mechanism, inter-annual changes in temperature patterns were capable of causing changes in salmon growth and survival (Figure 11). There was little variation in growth of salmon leaving British rivers during the 1970's, but greater variations in predicted lengths were calculated for the 1980's and 1990's. Smolt years 1982, 1986 and 1993 were particularly noticeable for having reduced lengths. The North Atlantic Oscillation (NAO) for these periods was mainly positive, indicating that changes in oceanographic conditions may have predictable impacts on salmon growth and survival. Calculated lengths were compared with the mean of the monthly NAO index for the time when each salmon was in the ocean. Results showed that calculated lengths generally increased as NAO decreased (Figure 12).

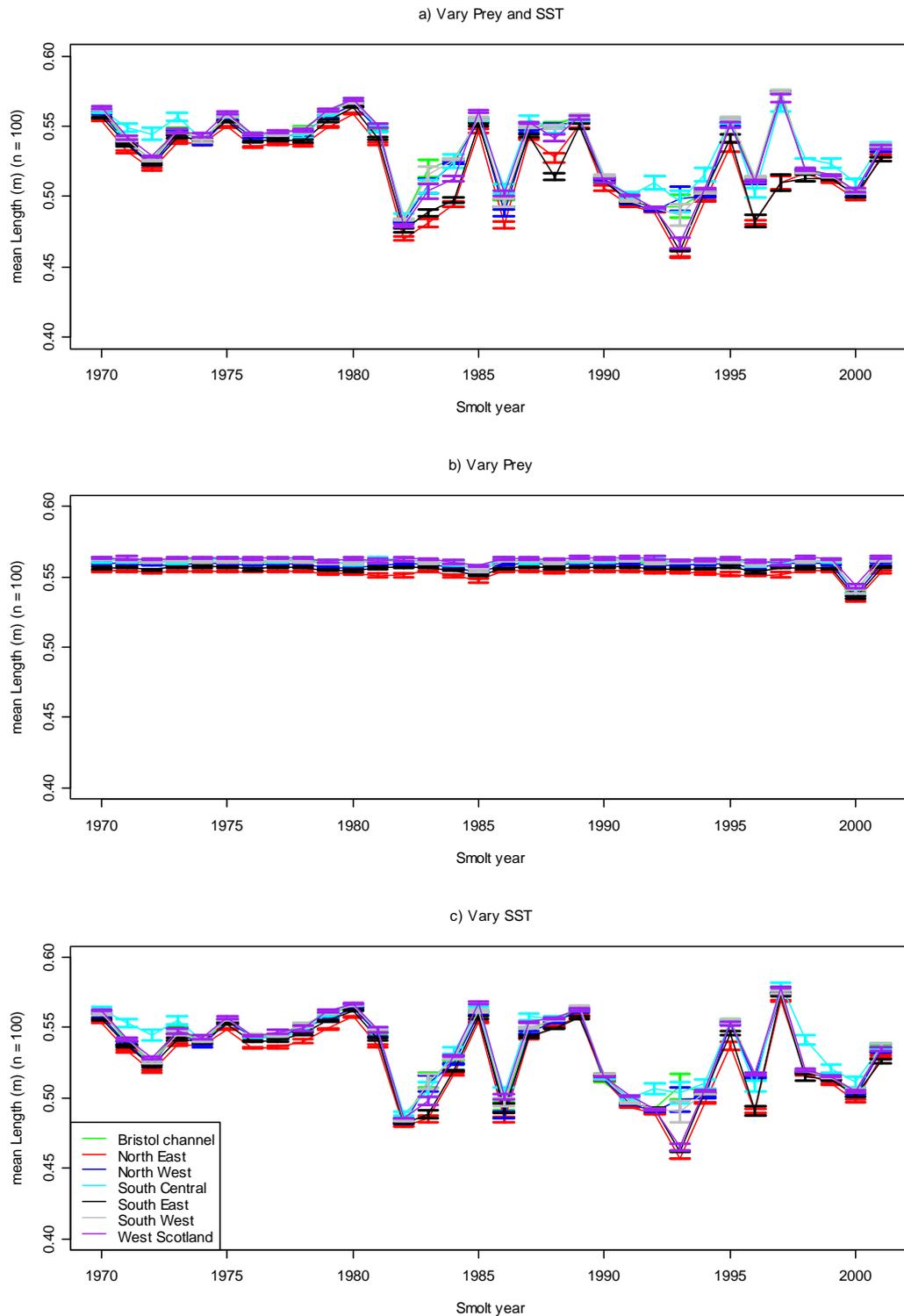


Figure 11. Mean length of salmon (n = 100) on the 15th of August using thermotaxis from 7 different rivers given a) SST and prey from 1970 to 2001 b) prey from 1970 to 2001 SST from 1970–1971 and c) SST from 1970 to 2001 and prey from 1970–1971. All currents set using 1993–1994. Bars show 95% confidence intervals.

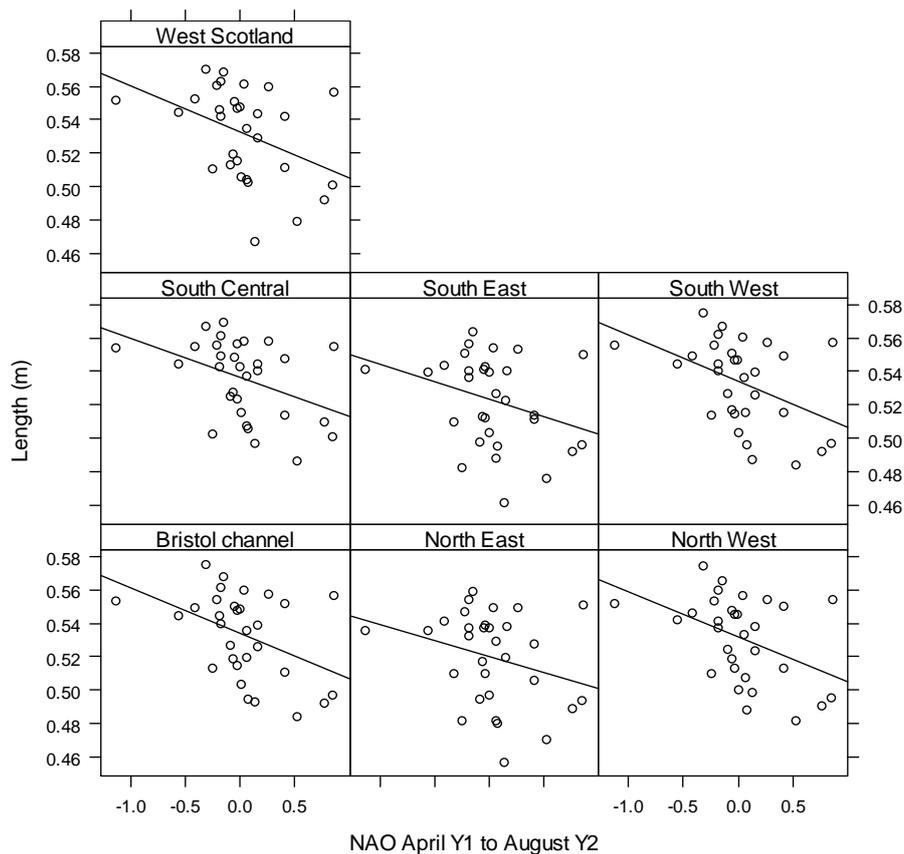


Figure 12. Mean of the monthly April year 1 to August year 2 NAO index versus calculated lengths for salmon using thermotaxis.

The model was used to predict the effects of inter-decadal variations in future SST on calculated lengths, depending on variations in prey availability and regardless of changes in local currents, when the simulated salmon followed the same fixed trajectories. The bioenergetic model, together with future predictions of ocean surface temperature, were used to simulate growth of salmon that might occur in the period 1990–2100 as a result of one scenario for future climate change (i.e. observed anthropogenic emissions to 1990 and the IS92a 'business as usual' scenario thereafter) (Johns et al., 2003). Results showed that, given fixed trajectories and steady swimming speeds, increases in temperature would lead to an increase in growth as the salmon experienced warmer temperatures that created more favourable conditions for growth regardless of prey availability (Figure 13). This was because more energy was gained through increased consumption than was lost through increased respiration. These results suggest that, if all other factors are equal and salmon are following set routes, they will not be adversely affected by climate change driven future increases in SST. Given this modelled behaviour, the only factors that could cause an adverse effect as a result of climate change are a decrease in prey availability, altered timing of smolt emigration, or a change in current patterns.

A different result was found when thermotaxis was implemented to simulate the type of behaviour that might result when the salmon were attempting to react to the local conditions. Under this particular migration scenario increases in temperature lead to a slight decrease in growth (Figure 14). Many of the simulated salmon were able to adapt to the change in oceanographic conditions by seeking similar conditions elsewhere in the ocean (Figure 15). This suggests that, during their oceanic phase, salmon may be capable of adapting to future climate change. However, predicting the effects of climate change on salmon growth and survival is limited by a lack of detailed information on the behavioural mechanisms controlling salmon migration in the open ocean. For example, salmon from the north east and south east of England were more impacted by the long-term changes in SST than the other home-rivers (Figure 14). This was partly because the east coast salmon attempted to swim into areas of faster currents in order to find areas with the appropriate temperatures in comparison with west and south coast salmon. Therefore east coast salmon entered areas with less prey and shorter days. They also had to use more energy to swim against the stronger currents. Collisions with land were also a contributing factor to this east-west bifurcation in the results. Under this migration scenario the salmon used a great deal of energy attempting to find the appropriate temperatures conditions; they attempted to swim along temperature gradients in order to find areas with these conditions. Where a temperature gradient (e.g. toward cooler water) lead a salmon to encountered land, the salmon would continually swim toward the cooler water. Therefore simulated salmon that encountered land used far more energy attempting to find cooler water, but instead collided with the coastline.

This was the situation for salmon travelling from the east coast, who travelled towards the Scandinavian coastline in an attempt to find the appropriate temperature conditions (Figure 16). In this case warmer temperatures also meant that more energy was used because respiration losses are increased in warmer conditions. Modelled encounters with the coastline may be an artefact of the model which is not currently representative of real-world salmon behaviour. Improvement and testing of the behavioural mechanism controlling migration is therefore an area for future research.

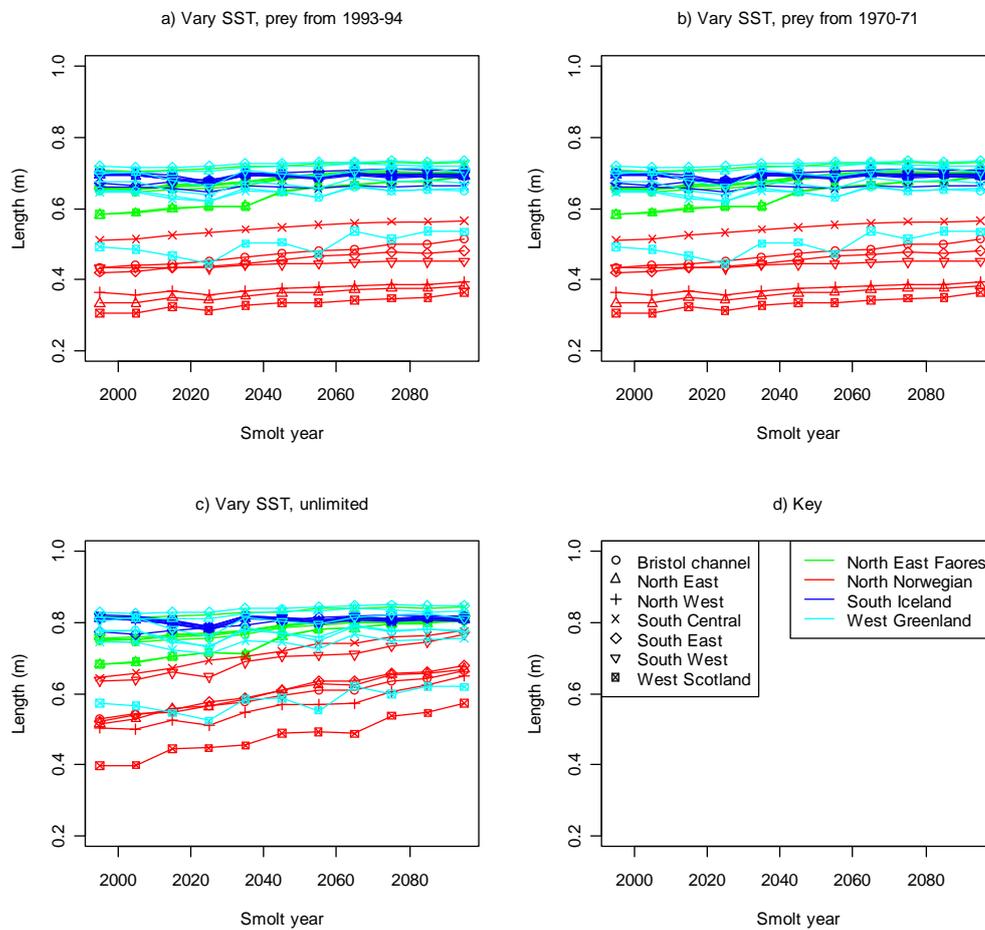


Figure 13. Lengths of salmon on the 15th of August using fixed trajectories given decadal-averaged temperature regimes from 1990 to 2100 a) prey set using 1993–94, b) prey set using 1970–71 and c) unlimited prey (all currents were set using 1993/1994 sea winter).

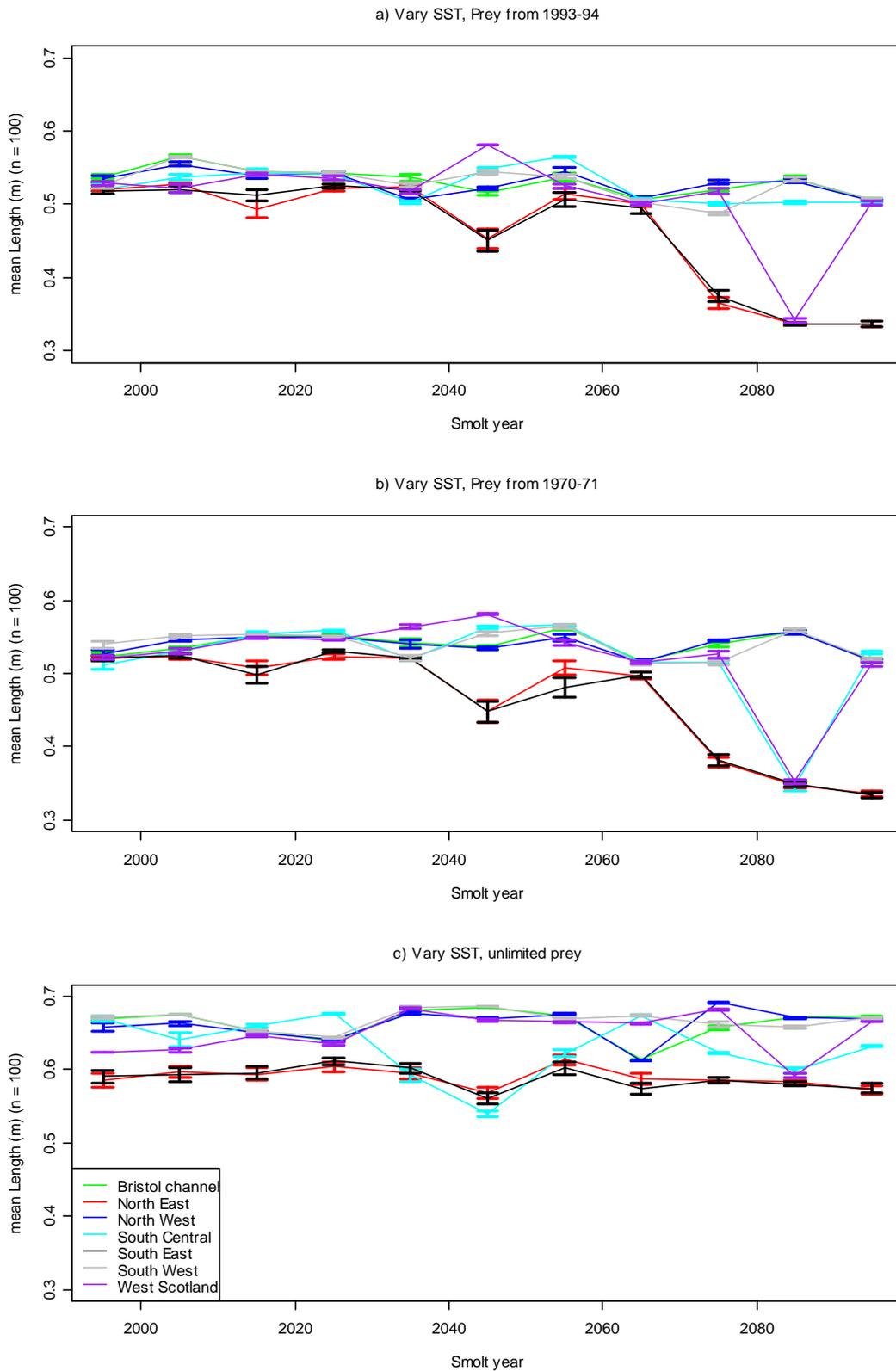


Figure 14. Mean length of salmon on the 15th of August using thermoregulation from 7 different rivers (n = 100) given decadal-averaged temperature regimes from 1990 to 2100 a) prey set using 1993–94, b) prey set using 1970–71 and c) unlimited prey (all currents were set using 1993/1994 sea winter). Bars show 95% confidence intervals

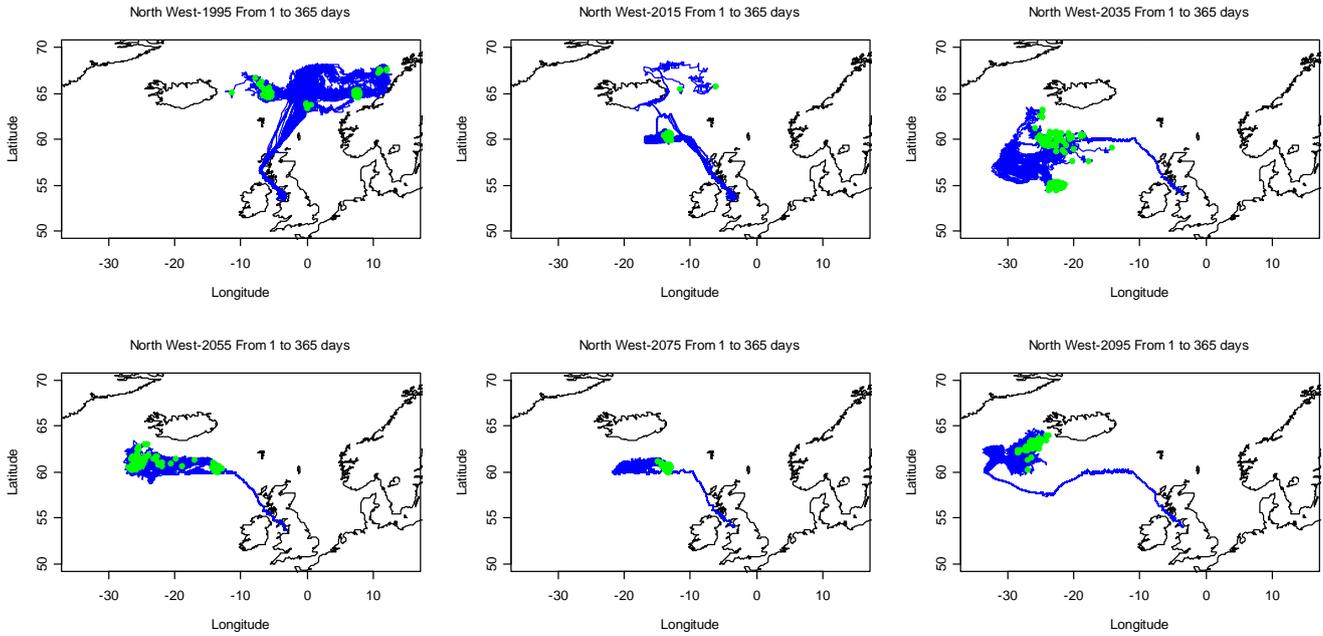


Figure 15. Affect of climate change in the positions of 100 salmon using thermotaxis that left the north west of England. Green dots indicate positions after 365 days.

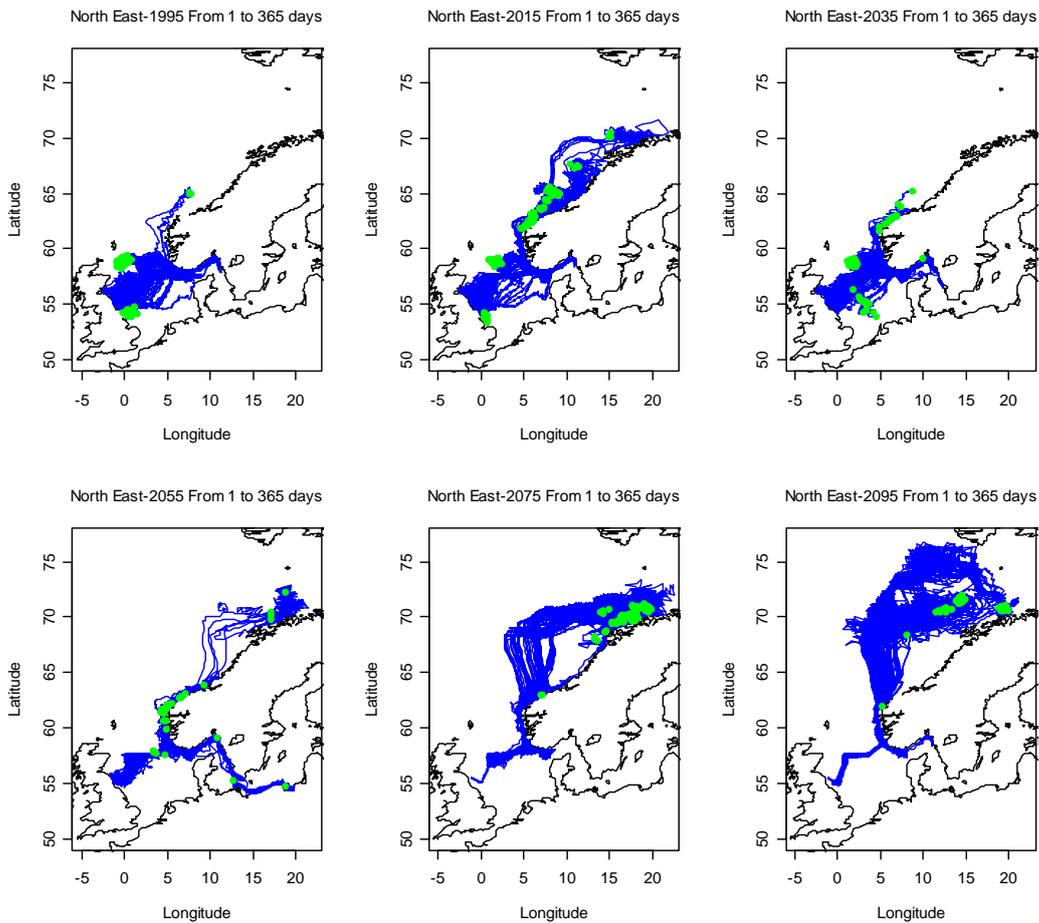


Figure 16. Affect of climate change in the positions of 100 salmon using thermotaxis that left the north east of England. Green dots indicate positions after 365 days.

Reliability of the results

This project used a physiologically and physically-based numerical modelling approach to develop an individual-based bioenergetic model, which predicted the growth and survival of migrating Atlantic salmon. The individual-based Lagrangian model was then deployed within an Eulerian marine environment to assess the relative

importance of both future and past inter-annual variations in temperature, prey availability and surface currents on the growth of Atlantic salmon. The advantage of this type of approach is that it allows incorporation of many biological processes and has great potential for increasing understanding of the mechanisms controlling salmon growth and survival. However, adopting this approach meant that the model contained many different parameter values, options and scenarios that could be explored. Thus there are several sources of uncertainty that should be considered when interpreting the model results. We attempted to reduce, or investigate, the effects of these uncertainties using several techniques and approaches:

- a) Where possible we used published information on adult Atlantic salmon to parameterise the bioenergetic model. Appropriate statistical methods (e.g. major axis regression) were used in cases where parameters were derived from observed data.
- b) Sensitivity experiments were carried out in order to demonstrate the effect of altering the physiological parameters within the bioenergetic model.
- c) Sensitivity experiments were carried out in order to apply a robust investigation of the dominant mechanisms and controlling factors within the spatial bioenergetic model.
- d) Where the appropriate data were available, comparison between observed data and model predictions were made for both the positions and the lengths of migrating salmon. Results showed good correspondence between observations and calculated lengths given the limited data available (e.g. Figure 7).
- e) We demonstrated that, given sufficient information on the mechanism controlling behaviour, it is possible to predict salmon migration trajectories, growth and survival. However, lack of understanding of the migration behaviour is a great source of uncertainty within this process. When investigating the effects of changes in oceanographic conditions on salmon growth and survival, we compared results calculated using contrasting behaviours.
- f) We investigated several interacting oceanographic factors which might be affecting salmon populations. We attempted to separate out the affects of inter-annual variations in prey, temperature and surface currents for salmon from different rivers and using different behaviours. This was achieved using controlled numerical experiments. Appropriate statistical methods (e.g. analysis of variance) were applied in order to analyse the results.

Future research recommendations

- a) Physical experiments

The bioenergetic model developed in the present project predicts migration routes, growth in length and weight and bioenergetic 'survival' of Atlantic salmon, *Salmo salar*, in the north Atlantic Ocean in relation to time and size of sea entry, oceanic conditions and behavioural options. It was desirable to 'validate' the model, in the sense of assessing the reliability of its output for its intended purpose (predicting likely changes in salmon populations to inform policy advice). This has been done in a restricted way using sensitivity analysis and by comparing output with the limited available field data on migration and growth, but there is scope for further testing of the physiological aspects of the model under controlled conditions. Physiological studies are needed both to 'calibrate' the model (revise the parameters of some of the major bioenergetic functions) and to test predictions of growth rate estimates for post-smolts in sea water.

A protocol for a growth trial under combinations of temperature and swimming speed was outlined. Two experimental sites in the UK have the facilities required to support this work: the CEFAS Weymouth laboratory and the University of Stirling's Marine Environmental Research Laboratory, Machrihanish. The growth trial study is anticipated to take 2 years, or 3 years if the calibration studies were to be included. The main costs of the project would be scientific staff time, fish procurement and transport, facility charges (tank space, temperature control, fish husbandry, fish feed) and travel and subsistence for visits to suppliers and the experimental facility. Other costs would include scientific equipment and consumables, training, Home Office project and personal licences, and overheads.

- b) Data availability

Overall, results indicated that predicted changes in marine conditions resulting from future climate change are capable of causing a change in the growth and survival of British salmon populations. However, our understanding of migration behaviour is limited by the paucity and limited availability of observed data of salmon growth and movements in the open ocean. We obtained observed data on salmon tagging experiments and catch data from several sources through personal communication. We recommend that data already collected as part of salmon monitoring experiments be more widely advertised and accessible. There is a particular lack of information on the migration patterns and behaviour of Atlantic salmon. Although some information was available on the recapture locations of tagged salmon it is difficult to infer which direction-finding mechanisms are being used by the real salmon when only a small number of spatially discrete observed locations are available. There is

also a lack of information available on the sampling strategies used to recapture tagged salmon. Having conducted this research we recommend increased availability of tagging data from “index rivers”.

It is crucial that any present salmon population monitoring strategies be maintained, and where necessary improved, if the early warning signs of climate change are to be detected. This project demonstrated that it may be possible to link changes in salmon growth and survival with oceanic phenomena (e.g. the NAO).

There are several types of monitoring where improvements would be beneficial. These include post-smolt surveys in coastal waters and monitoring of bycatch in pelagic fisheries.

c) International collaboration

Better international collaboration between scientists may also be beneficial. At a recent international conference of hydro-ecology presentations were made by several scientists working on research relating to threats to salmon populations. Particularly relevant work is taking place in Norway and Sweden (e.g. Jonsson et al., 2006, Saltveit et al., 2006).

d) Analysis of oceanic conditions and long-term salmon data

We demonstrated the patterns in the bioenergetic model were linked to patterns in the NAO (North Atlantic Oscillation). Further analysis is required in order to investigate empirical relationships between historical records of salmon catch, salmon sizes and physical oceanographic conditions. This could lead to identification of patterns that could then be used to test the results shown here and predict the effect of future climate change on salmon populations.

e) Whole life-strategy modelling

We assumed that entry to the ocean was on the 14th April for all salmon in all years and in all locations. We also assumed that all salmon were the same size on entry to the ocean. In reality size and date of entry to the ocean will be affected by climate change. For example, currently salmon from more northerly locations enter the ocean later in the year in comparison with more southerly populations. This means that salmon populations could adapt to climate change during their freshwater as well as their marine phases. The model that was developed for this project only considered the marine phase of the salmon life-cycle. Future work could be developed to link the marine and freshwater life-stages. This would allow better understanding of the combined effects of climate change on both the freshwater and oceanic phases on salmon whole life-history strategies.

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- Anton Ibbotson (CEH): River Frome smolt size and date data.
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References to published material

9. This section should be used to record links (hypertext links where possible) or references to other published material generated by, or relating to this project.

Project outputs

Year 1

Booker, D.J., Wells, N.C., Smith, I.P. (2003) Modelling the bioenergetics of (marine) salmon migration. Presentation given to DEFRA staff visiting CEH-Wallingford, April 2003.

Booker, D.J., Smith, I.P., Ward, P., Wells, N.C. (2003) Modelling the bioenergetics of (marine) salmon migration. Presentation given at DEFRA review of Salmon and Freshwater Fisheries Research programme, CEH-Wallingford, July 2003.

Year 2

Booker, D.J., Ward, P.E., Wells, N.C., Smith, I.P. (2004), Modelling atlantic salmon growth and survival. Poster presented at UK-GLOBEC, Ecosystem dynamics in the ocean, Royal Society, London, February 2004.

Ward, P.E., Wells, N.C., Booker, D.J., Smith, I.P. (2004), Building virtual marine environments for salmon migration models. Poster presented at European Geophysical Union Conference, Nice, April, 2004.

Wells, N.C., Ward, P.E., (2004), How good is OCCAM at estimating surface drift in the North Atlantic? Oral paper presented at European Geophysical Union Conference, Nice, April, 2004.

Booker, D.J., Ward, P.E., Wells, N.C., Smith, I.P. (2004), Modelling marine phase growth and survival of migrating atlantic salmon. Presentation given at NERC-EPSCRC Workshop on Uncertainty, Complexity and Predictive Reliability of Environmental/Biological Models. University of Nottingham, April 2004.

Year 3

Wells, N.C., Booker, D.J., Smith, I.P., Ward, P.E. (2005), Modelling atlantic salmon growth and survival. Poster presented at Dynamic Planet Conference, Cairns Australia, August 2005.

Year 4

Booker, D.J., Wells, N.C., Ward, P., Smith, I.P. (in review). Modelling the effects of ocean surface currents on the trajectories of migrating Atlantic salmon, *Salmo salar* L.. *Canadian Journal of Fisheries and Aquatic Sciences*.

Booker, D.J., Smith, I.P., Wells, N.C., (in prep). Individual-based bioenergetic modelling of post-smolt salmon migration. *Ecological Modelling*.

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