UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

School of Ocean and Earth Science

The marine life of Atlantic salmon: evidence from the chemistry of scales

by

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ABSTRACT

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES
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This research provides a new method to identify likely marine feeding grounds for migratory pelagic species that are problematic to directly study at sea. The method is based on stable isotope compositions of tissues that may be sampled without harming the target animals, and can be conducted retrospectively from tissue archives.

The wild Atlantic salmon has been in steep decline throughout its native range over the past four decades, largely due to increases in marine mortality. This research investigated potential causes of this decline using stable isotope analysis of archived scale samples, taken from returning adult salmon over the past few decades. Investigations of UK scale holdings identified the River Frome and Northeast Coast Driftnet Fishery archives as the most available and useful, giving good spatial contrast and temporal coverage.

After developing sampling and analytical protocols, carbon and nitrogen isotopic composition was measured in grilse (one-sea winter) and multi-sea winter (MSW) salmon scale samples taken from both archives over 23 and 14 years. Analyses were performed on the last marine growth season, giving a retrospective record of marine conditions experienced by each fish. Both isotopes are influenced by baseline environmental conditions, and climatic effects are found to exert strong controls on numbers of fish returning to both the Northeast Coast and River Frome populations. Trophic level and/or baseline nitrate effects are also found to influence returning abundance to these populations, although more strongly in the Frome. Yearly $\delta^{13}C$ values were correlated with median yearly sea surface temperature values for each degree of latitude and longitude across the North Atlantic, and maps produced of the correlation strengths. These maps suggest likely feeding grounds for each cohort within each population, with the River Frome grilse and MSW salmon respectively feeding near the shelf breaks of northeast and southwest Iceland. The Northeast Coast grilse and MSW salmon were, in contrast, feeding near the shelf breaks of the southern Norwegian Sea and the Bear Island Trench in the northern Norwegian Sea, respectively.

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DECLARATION OF AUTHORSHIP

I, Kirsteen MacKenzie

declare that the thesis entitled

The marine life of Atlantic salmon: evidence from the chemistry of scales

and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
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- where I have consulted the published work of others, this is always clearly attributed;
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- none of this work has been published before submission

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1. Thesis introduction

Since the Industrial Revolution there has been major overall decline in the populations of wild Atlantic salmon (*Salmo salar,* L.) throughout their range (Cowx & Van Zyll De Jong 2004). The factors contributing to this decline are of great concern as the salmon is a valuable fish, both economically and ecologically. The total fishery value for migratory salmonids in England and Wales alone was estimated (Anon. 2001) at £128 million per annum, as the salmon is important to both commercial and to recreational fisheries. The value to local economies of each individual rod caught salmon was calculated almost two decades ago as approximately £5000 (Radford et al. 1991). In terms of ecological value, returning salmon provide essential nutrient input from both gametes and carcasses to the trophic web of freshwater rivers and streams, including to resident juvenile salmon (Jonsson & Jonsson 2003a), while the resident juvenile salmon may themselves be an important resource to a wide range of piscivores (Koed et al. 2006).

This thesis provides an overview of the life history of the Atlantic salmon and the decline in their numbers over the past three decades, followed by the methods used to investigate possible reasons for this decline. Many factors have been implicated in the decline of wild Atlantic salmon, including riverine habitat degradation, genetic dilution and disease caused by fish farming, overfishing and climate change, but it is still not clear whether any of these factors are the main causes, or if each affects different stocks in different ways. In particular, it appears that the majority of decline over recent decades has occurred in the numbers of fish returning from sea, i.e. the marine phase of life (Cairns 2002; Friedland et al. 2005; Friedland et al. 2009; Jonsson & Jonsson 2004a; Peyronnet et al. 2007). Despite vast resources and decades of study devoted to this species, relatively little is known about the marine phase (Friedland 1998). The research detailed in this thesis seeks to address this lack of knowledge. The results obtained are presented and discussed in the light of current knowledge of salmon ecology, together with proposed explanations for the patterns shown. The conclusions made consider the implications of these results to fish research, and suggest areas of work that might be addressed in future.

1.1 Life history of salmon.

The Atlantic salmon is an anadromous teleost (fish which hatch in rivers, migrate to mature at sea, then return to rivers for spawning) of the family Salmonidae. It has been heavily studied, due largely to its importance as a commercial and recreational fish across the North Atlantic (Marschall et al. 1998). Despite its international significance, there is a paucity of knowledge concerning the drivers of population change and persistence, particularly in the light of major population declines since the 1970s. A schematic summary of Atlantic salmon life history is shown below, in Fig. 1.1.

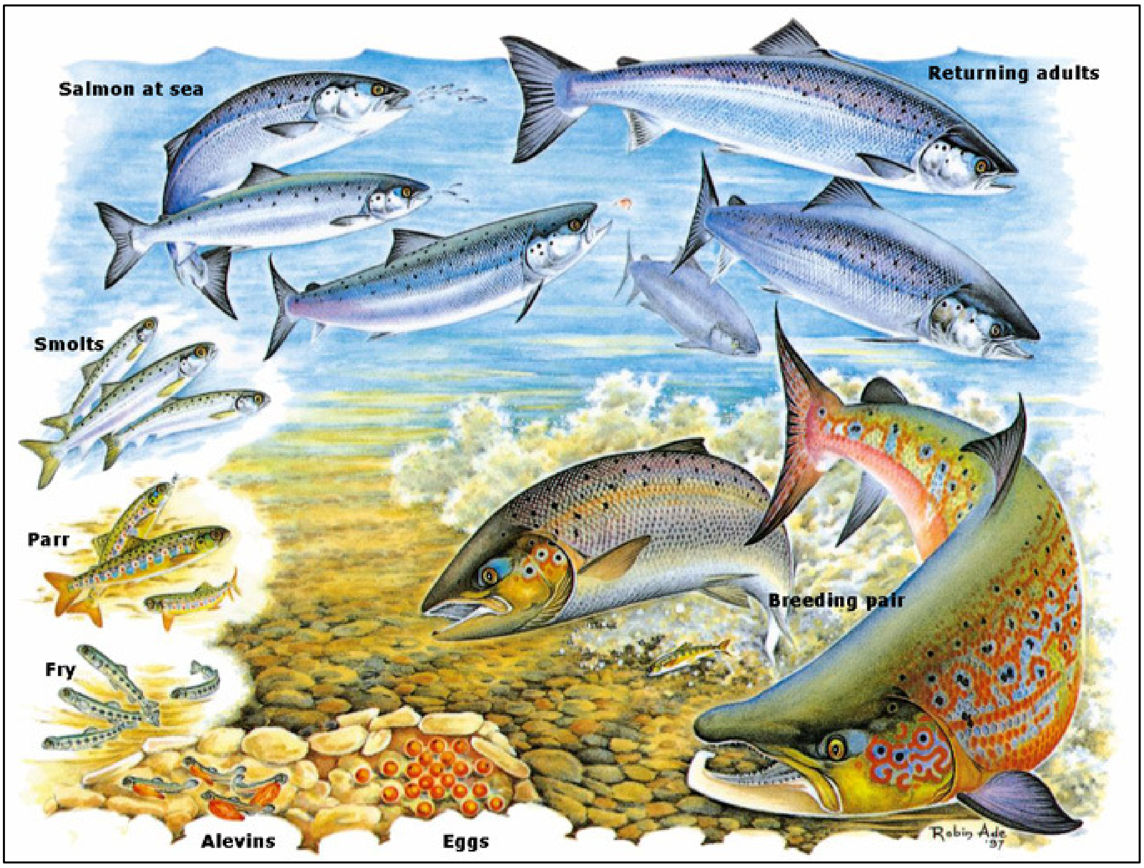


Figure 1.1. Illustration representing the life cycle of the Atlantic salmon (The Atlantic Salmon Trust © 2010).

Evolution and native range

The current population structure of the Atlantic salmon is less than 10,000 years old, as populations re-colonised to their present ranges after the last Pleistocene deglaciation. In Europe, the natural modern range extends from northern Russia to southern Iberia (Nicieza et al. 1994; Verspoor et al. 1999), see Fig. 1.2.

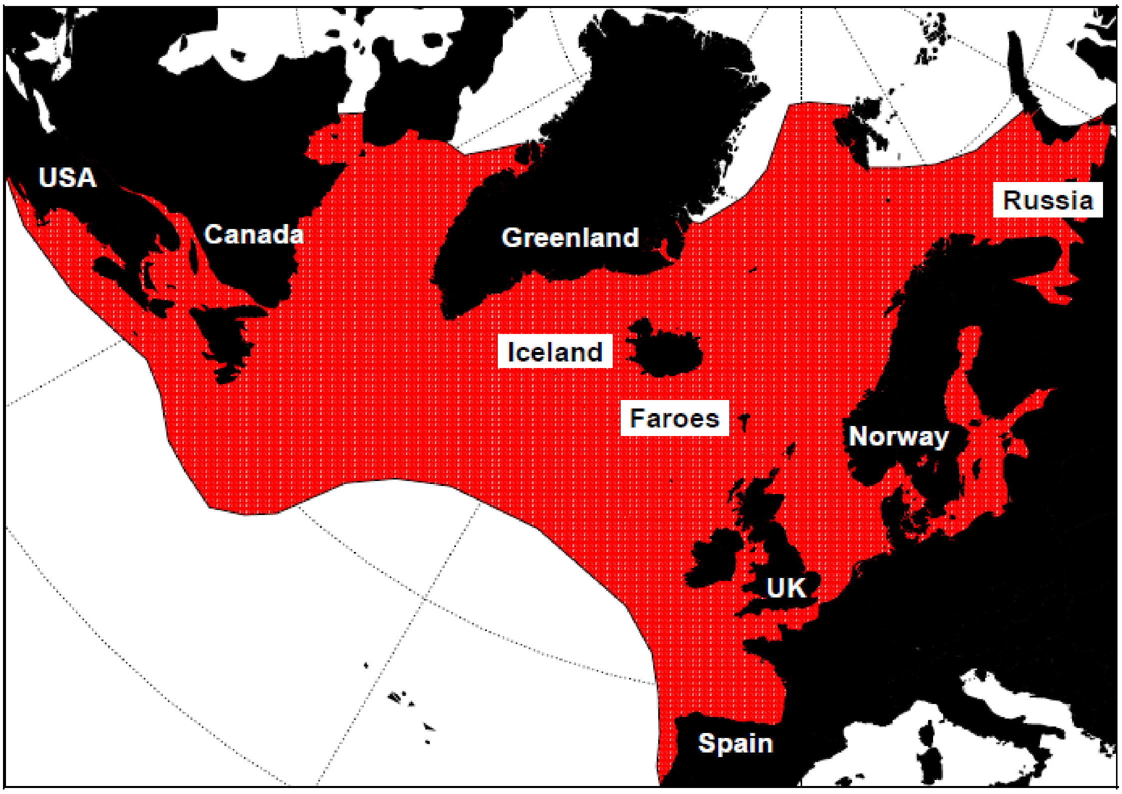


Figure 1.2. Geographical distribution of salmon in the North Atlantic (ICES 2007).

Based on mitochondrial DNA analyses, it is thought that *S. salar* re-colonised its modern European range from at least one, possibly two glacial refugia (Verspoor et al. 2005). River populations in southern Europe, the British Isles, Norway and northern Russia appear to derive from the Iberian peninsula refugium, while Baltic and Icelandic river populations are proposed to originate from a southern North Sea glacial lake, into the Baltic Sea approximately 10,000BP, then onto Iceland c.2,000 years later (Verspoor et al. 1999). This relatively brief history of current species population structuring has not given time for speciation, but has allowed, through phenotypic plasticity, for localised adaptation to natal ranges, e.g. differential pH and temperature tolerance ranges. This has led to great genetic disparity between populations that have evolved to suit local catchment conditions (Donaghy & Verspoor 1997; Garcia de Leaniz et al. 2007; Verspoor et al. 2005; Verspoor et al. 1999).

Life stages in freshwater

Eggs and alevins.

The eggs of Atlantic salmon are unusual in that they are relatively large, are buried in nests known as redds, built and guarded by the females in their natal streams, and are incubated for comparatively long periods of time. Spawning usually occurs in autumn-winter, and fry emerge the following spring. Egg size and nest guarding are correlated with higher survival rates to the fry stage (Marschall et al. 1998). The number and size of eggs are proportional to the size of the female; therefore larger, older females tend to have greater reproductive success (Berg et al. 2001; Elliott & Hurley 1998; Fleming 1996; Hendry et al. 2001; Marschall et al. 1998). Salmonids have much larger eggs relative to many other teleost fish, stemming from greater maternal investment. This investment should theoretically lead to a developmental advantage for newly-hatched salmonids over other teleosts, but also results in lower fecundity for these species (Marschall et al. 1998). In order to produce large quantities of milt and provide the resources for such large eggs, salmon begin to self-catabolise on their return migration to spawn, ceasing to feed during this journey until their return to sea some months later (Doucett et al. 1999a). Each female excavates and lays eggs in several redds throughout the breeding season.

The eggs require high flow rates to provide sufficient aeration and oxygen levels during incubation, and are thus at risk from silt loading, eutrophication and pollution (Jezierska et al. 2009; Soulsby et al. 2001; Vuori et al. 2008). The rates of development from embryo to hatching, and lecithotrophic alevin to emergence from the spawning gravels as actively feeding fry, vary inversely with ambient water temperatures (Elliott & Hurley 1998; Malcolm & Soulsby 2002). Depending on the riverine conditions, particularly prey or habitat availability and flow volume following emergence from the gravels, the above factors can influence both the growth and smolting times of the juvenile salmon (Arnekleiv et al. 2006; Imre et al. 2010; Riley et al. 2009).

Fry.

On emergence from the gravel redd, salmon fry have relatively specific habitat and territory requirements, tending to occupy regions of high flow velocity (Marschall et al. 1998) due to increased prey availability and oxygen levels. Fry move downstream after emergence until they find an unoccupied region of suitable habitat (Matthews et al. 1997). According to the theory of ideal free distribution (Fretwell 1972), fry arrange themselves in the stream according to the nearness and availability of optimal habitat, with weaker individuals forced further downstream or into sub-optimal habitat patches (Einum et al. 2008). This has implications for both timing of emergence and survival, with larger, earlier emergent fry establishing and competing for territory more effectively (Einum & Fleming 2000).

Parr.

The pattern of density dependent distribution, extending from ideal territories down an optimality gradient of available habitat, continues through the ill-defined point at which the fry become parr (Youngson & Hay 1996). The duration of the parr stage, identifiable by a pattern of dark banding on the flanks of the fish, is very variable, comprising between one and eight years (Marschall et al. 1998). During this time the fish will grow and eventually smolt in preparation for the seaward migration. Some so-called precocious parr will, however, mature in freshwater and be able to fertilise the eggs of returning adult female salmon, or, very rarely, be mature females capable of egg-laying. Such cases of early maturation are dependent on lipid storage levels reaching a certain threshold in the year, thought to be around May (Rowe et al. 1991). If lipid levels do not reach this threshold, the salmon will continue to grow and eventually smolt, as will the precocious parr post-spawning.

Cover remains important as refuge both from predators and from the energetic costs of remaining in high flow velocity (Stickler et al. 2008). At this parr stage, water acidification is also very important as it can delay or stop the smoltification process, leading to impaired osmoregulatory ability on exposure to seawater and therefore lower survival (Kroglund & Staurnes 1999; Waiwood et al. 1992). The habitat and quality of resources available at the parr stage are very important in shaping the life history trajectory; those with better access to resources will be larger and have higher survival rates to seaward migration, and are ultimately more likely to have reproductive success (McGinnity et al. 2007; Youngson & Hay 1996).

Smoltification and smolts.

A combination of size and photoperiod has been shown to instigate smoltification, the process by which the freshwater parr become silvered with guanine and develop the osmoregulatory ability to respire in seawater (Bjornsson & Bradley 2007). Olfactory sensitivity peaks at the start of smoltification and shortly afterwards, when imprinting to natal streams is thought to occur (Dukes et al. 2004; Morin & Doving 1992). There is a continuum of river ages through the Atlantic salmon's freshwater geographical range before smoltification, with fish towards the south tending to spend less than two years in rivers, and fish at higher latitudes spending up to eight years before smolting (Marschall et al. 1998). This latitudinal effect is largely explained by feeding and growth opportunities, which are in turn strongly controlled by temperature and photoperiod; salmon are visual predators and feed only during daylight in freshwater, but growth is related to temperature in a parabolic manner, increasing towards optimal temperatures, then decreasing towards the upper limit of thermal tolerance (Metcalfe & Thorpe 1990).

The UK is approximately in the middle of the European salmon range, thus median age and growth might be expected, with more southerly stocks showing characteristics of lower latitude salmon, and stocks from the north of the UK demonstrating similarity to those of, for example, southern Norway and Sweden. Atlantic salmon parr in the UK generally fall into two size classes, with the faster growing, larger size class tending to smolt at age 1+, and the smaller, slower growing size class at age 2+ the following year (Thorpe et al. 1982); this is likely due to the energetic stresses of migration, requiring sufficient levels of stored lipids and muscle mass for transition from fresh to salt water, and for successful migration to the sea (Stefansson et al. 2003). The process of smoltification is also likely related to lipid storage, as individuals with higher energy reserves tend to smolt earlier (Rikardsen & Elliott 2000). Other factors thought to contribute to anadromy and smoltification are differential habitat incentives, sex, and population density in resource-limited environments (Doucett et al. 1999b; Taylor & Bentzen 1993). Anadromy is a more successful strategy under greater population densities, where there is increased competition for both territory and food. Larger fish with greater lipid reserves have greater ability to make a successful transition to the marine environment where competition for space and food resources is decreased (Jonsson & Jonsson 2005; Jonsson & Jonsson 2003b), leading to overall greater reproductive potential success (Doucett et al. 1999a).

Early post-smolt migration

The conditions encountered by smolts entering estuarine environments are thought to be important controls on the rate and nature of the out-migration. Lower temperatures may delay sea entry, but smolts move largely with the prevalent surface currents in estuaries (Anderson 1997; Hansen et al. 2003; Holm et al. 2003; Moore et al. 1998a; Moore et al. 1998b; Moore et al. 1995), causing unavoidable stress if unfavourable conditions are encountered. Once at sea, salmon appear to use northward flowing currents, e.g. those along the European continental shelf edge, to aid active swimming to nursery and feeding grounds in the north Atlantic (Atlantic Salmon Atlantic Salmon Federation 1997-2007; Booker et al. 2008; Hansen et al. 2003; Turrell

& Shelton 1993). Slower growing post-smolts may be forced to remain in less favourable areas until they are large enough to actively migrate to areas with more optimal temperatures and feeding opportunities (Friedland et al. 1999; Friedland et al. 2000).

Marine location and diet

Salmon are obligate pelagic fish in the marine environment, remaining largely in the upper ten metres of the water column where the majority of their prey species are found (Mills 2003). This means that their diet is limited to appropriately-sized fauna in the upper pelagic food web of the North Atlantic. Salmon prey items at sea generally consist of zooplankton, mostly crustacea, and smaller fish, largely chosen based on size and potentially tempered by competition with other pelagic fish species such as herring and Norway pout (Hansen et al. 2003; Holm et al. 2003), although these species also form important prey.

It is thought that Atlantic salmon use a combination of currents and active swimming when migrating (Booker et al. 2008; Moore et al. 1998a; Moore et al. 1998b). Fig. 1.3 shows a schematic of the major ocean currents in the North Atlantic. Salmon entering the Atlantic from English rivers will experience a prevailing northward directionality from the North Atlantic Current. This current divides into two parts to the north of Ireland along the European Continental Shelf edge; the northeasterly part becomes the Norwegian Current and flows into the Norwegian Sea, and the northwesterly part splits again to flow to the south of Iceland or towards Greenland. These currents can be used to investigate hypotheses on the likely migration routes of salmon on entering the Atlantic Ocean.

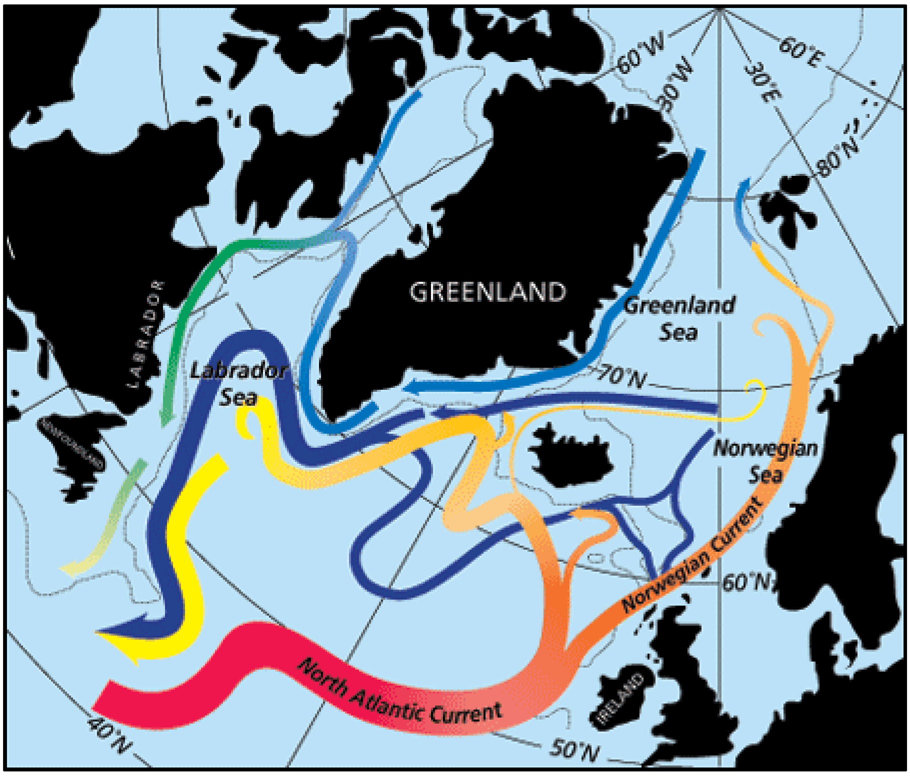


Figure 1.3. Schematic of the major currents, and the directions in which they flow, circulating in the North Atlantic Ocean (McCartney et al. 1996).

Current perceived locations of Atlantic salmon at sea are based largely on work done on radioisotopes, scale reading and tagging data. Radiocaesium studies have been used to determine movements through inference of salmon feeding locations, based on the strong east-west gradient of ^{137}Cs in the North Atlantic due to European anthropogenic inputs to surface waters (Spares et al. 2007; Tucker et al. 1999). Migration data from radiocaesium studies have proven controversial, however, due to the short timespan claimed for large migrations, and are quite non-specific in geolocating feeding grounds (ICES 2007). Scale characteristics are also commonly used to determine the origin of salmon from fishery samples. Many studies (e.g. Friedland et al. 1999; Lear & Sandeman 1980; Reddin 1986; Reddin et al. 1988) have used discriminant function analyses of freshwater and marine growth patterns on scales to identify salmon at sea to continent, and often country of origin.

Combined with the above movement analyses, there has been a concerted effort in most Atlantic salmon producing countries to tag large proportions of hatchery fish and outgoing wild smolts (ICES 2007, 2008b, 2009c). Tag-recapture studies are confounded by a number of issues, particularly a lack of data from outside fishing times and areas. Approximately 3.75 million salmon were tagged in England and Wales between 1958 and 2007, c.250,000 up to 1984 with external tags, and 3.5

million with coded wire microtags (CWTs) from 1985-2007 (3.3 million hatchery fish and c.200,000 wild smolts), with doubtless many more to date. Of these millions tagged, only 2,292 salmon from England and Wales combined (0.06%) have been recaptured outside England and Wales homewaters (ICES 2008b, 2009c), see Tables 1.1 & 1.2. This recapture figure is slightly misleading as the majority of recaptures (1,830 fish) were from Ireland, Northern Ireland and Scotland, where salmon may have been intercepted making the return migration; if these more local figures were to be removed from the total, only 462 recaptures remain, or 0.01% of all fish tagged in England and Wales.

Table 1.1. Summary of tag recoveries, by river, in fisheries outside UK(E&W) homewaters from salmon smolts tagged between 1958 and 1984; country codes are as follows; Gro: Greenland, Fr: Faroes, Cdn: Canada, No: Norway, Dk: Denmark, S: Sweden, Irl: Ireland, NI: Northern Ireland, & Sco: Scotland; rivers in bold represent areas sampled by the research detailed in this thesis (ICES 2007).

River	No. tagged	Tagging year	No. recoveries								
			Distant water		Other Areas						
			Gro	Fr	Cdn	No	Dk	S	Irl	NI	Sco
Coquet	**579**	**1968-69**	**1**								
Esk		**1980-84**	**3**	**15**		**3**		**1**	**2**	**2**	**22**
Ure	16,571	1968-79	104	1	3	2			2		
Avon	6,364	1968-71	18			1			4		
Frome		**1977-78**		**1**					**2**		
Axe	55,119	1960-71	90			1			2		
Exe	25.949	1968-71	36			2					
Dart	544	1968									
Taw	2,082	1968									
Severn	23,241	1958-64	7								
Wye	21,270	1958-64	5								
Usk	48,710	1958-73	44		1		1		28		
Lledr/ Erch/ Ogwen	1,816	1968-70									
Clwyd	639	1968-9									
Lune	563	1968									
Total (England & Wales)			308	17	4	9	1	1	40	2	22

Table 1.2. Summary of coded wire tag recoveries, by country of capture, in fisheries outside UK(E&W) homewaters from salmon smolts tagged between 1985 and 2006 (ICES 2007).

Year	Distant water		British Isles		
	Greenland	Faroes	Ireland	N.I	Scotland
1985			7		
1986	22	3	22	10	43
1987	17	7	66	61	10
1988	8	11	128	42	8
1989	12	9	71	4	32
1990	2	5	111	5	8
1991	3	8	57	3	1
1992	4	5	107	9	5
1993		3	101	5	6
1994		1	80	4	10
1995			148	2	28
1996			76	2	14
1997			44	5	
1998			36	2	
1999			117	4	
2000			113	4	
2001			54	3	
2002			41	2	
2003	2		27	0	
2004			8	0	
2005			10	0	
2006			9	1	
Total	70	52	1433	168	165

The studies detailed above have led to the commonly-held perception that salmon from England and Wales migrate to oceanic feeding grounds either around the Faroes or West Greenland (ICES 2009b). The majority of this precept is based upon only 378 tagged fish caught in Greenland and 69 in the Faroes (not separated into river of origin except pre-1985), over a period of almost 5 decades, that could be related back to country of origin through tag reading. These recaptured fish were caught only in traditional fishery areas and times; hence there is clearly a gap to be filled in the knowledge of salmon stock and population locations at sea.

Controls on return

Atlantic salmon may spend between 1 and 4 years at sea (Jutila et al. 2003). Individuals that spend only one winter at sea before returning to spawn are termed grilse, or one sea-winter (1SW) fish, while individuals that spend two or more winters at sea before return migration are termed multi sea-winter (MSW) fish. The cryptic nature of the marine phase of the Atlantic salmon's life history means that little is known about causes of variability in mortality that control return rates to rivers of origin; the fish are very difficult to study in the ocean because they are hard to find. It is therefore very difficult to determine whether there are particular reasons for patterns of mortality in the oceans. Generally speaking, reasons for intra-specific variability in population size may include age, size and sex structure, breeding capability and opportunity, health (Garcia de Leaniz et al. 2007) and exploitation rates (Godø 2003). In Atlantic salmon, these characteristics are very plastic, and may depend on factors such as stock genetics, river age (number of years spent in freshwater prior to out-migration) and sea age (number of years spent at sea prior to return migration), river and oceanic conditions, predation risk and prey availability (Godø 2003; Leggett & Deblois 1994; Turrell & Shelton 1993).

Salmon return to natal rivers to spawn, therefore the decision to return or to remain at sea is clearly linked to sexual maturation. It is thought that salmon have a minimum energy storage threshold required in order to mature (Jonsson & Jonsson 2004a; Jonsson & Jonsson 2003b), and that warm temperatures stimulate partitioning of metabolic energy towards lipid storage rather than protein production (Jonsson & Jonsson 2004a, 2005). The minimum maturation threshold of energy storage is lower for smaller salmon (Jonsson & Jonsson 2004b); Preferential lipid storage over protein production, e.g. in years of warmer summer temperatures leading to lower production, and therefore lower prey availability, may lead to both earlier and smaller maturation, and greater total rates of return (Turrell & Shelton 1993) through greater robustness to survive return migration. Lipid storage affects many life history stages in the Atlantic salmon; greater lipid reserves enable longer migrations and therefore the ability to move to more favourable habitats for both feeding and spawning, and also provide more reserves to produce gametes, subject to overall body size (Hendry & Beall 2004; Jonsson & Jonsson 2005; Marschall et al. 1998; Patterson et al. 2004). As a result, larger fish with higher lipid reserves are more fecund and more likely to be reproductively successful (Berg et al. 2001; Healey 2001; Marschall et al. 1998), and have higher rates of survival to return.

Return rates of grilse vs MSW

Salmonid migrations are induced by specific triggers, and call for specialised characteristics that enable tolerance for the stresses of the journey. Temperature acts as a cue for returning southward migrations, with grilse in particular moving south as northern waters cool. MSW fish may remain longer in colder waters, possibly due to their larger size providing enhanced temperature tolerance, and allowing them to exploit more favourable food resources (Turrell & Shelton 1993). This, together with migration time, may explain why only MSW fish are thought to make the journey across the Atlantic from Europe to the Labrador Sea and back (Hansen 1993; Hansen & Jacobsen 2003; Turrell & Shelton 1993). The total migratory distance to and from natal catchments (Jonsson & Jonsson 2005) and the length of time spent in freshwater on return are both strongly related to nutritional stress, as salmon cease active feeding on return migration and begin fasting on entry to freshwater, and do not feed again until their return to sea post-spawning (Doucett et al. 1999a). Both fasting and the energetic requirements of migration cause extensive catabolism of both stored lipids and proteins, for which the salmon must build up reserve pools in order to mature and migrate successfully (Jonsson & Jonsson 2005). If these pools are not at threshold levels, for example during colder years of reduced growth rates, maturation and return may be delayed. Thus returns of MSW salmon are more common following colder years at sea (Hansen 1993; Ritter 1993), and have been decreasing since 1970 (Ritter 1993).

1.2 History of populations

The large-scale decline in populations of *S. salar* has been most marked in the last three decades (Boisclair 2004; Boylan & Adams 2006; ICES 2005), see Fig. 1.4, and is attributed to a variety of causes, including freshwater habitat disturbance and destruction by factors such as pollution, siltation, and acidification (McCormick et al. 1998). However, much remediation work has been undertaken in the freshwater environment, and salmon are now shown to be returning to previously depopulated catchments (Cowx & Van Zyll De Jong 2004; Gerlier & Roche 1998). Stocks of Atlantic salmon, however, continue to decline despite improvements in freshwater habitats and significant stocking in freshwater catchments, indicating that the main causative factors occur at sea.

Potential causes of increased mortality in the marine environment include changes in oceanic conditions such as temperature, linked to prey availability, together with both direct and indirect fishing mortality (Boisclair 2004; Jonsson & Jonsson 2004a), which are all contributing factors in marine mortality and levels of recruitment (Mills 1993). The timing of entry to the marine environment is also strongly implicated in the success of the salmon, with survival and return rates linked to timing of primary production blooms, and therefore food availability (Anderson 1997; Koslow et al. 2002), which are in turn dependent on oceanic conditions (Beaugrand & Reid 2003).

Scale counting, fishery statistics, ICES models and direct tagging.

Due to its economic and social value, *S. salar* populations have been heavily monitored for signs of change throughout their natural range (Marschall et al. 1998). Despite this, causes of variation and decline are not well-constrained. Teleost scales are customarily used to determine age and growth in many commercially valuable fish, such as the Atlantic salmon, and accordingly archives are routinely stored in many places as a record of catches (Friedland et al. 2000; Friedland et al. 2009; Hutchinson & Trueman 2006; ICES 2007, 2009b, c; McCarthy et al. 2008; Peyronnet et al. 2007; Satterfield & Finney 2002). These scale archives, together with estimations of return rates, are an invaluable resource to provide information on the status of the population in terms of its spawning stock, age structure and returns success (ICES 1992). Scale archives compare well to other methods of monitoring, such as tagging and tracking, as scales integrate signals of diet and aquatic conditions throughout the lifetime of the fish, with minimal turnover, and may be used for life history analysis. Tagging and tracking studies, in contrast, are often prohibitively expensive and time-consuming, and reliant on recapture of marked fish, often with very low success rates (Lacroix et al. 2004; Smith et al. 1998). Tagging can also cause deleterious effects on the fish (Lacroix et al. 2004; Makinen et al. 2000), while scales can be sampled relatively non-destructively (Cunjak et al. 2005).

The International Council for Exploration of the Seas (ICES) Working Group on North Atlantic Salmon (WGNAS) produces a pre-fishery abundance (PFA) model annually to estimate returns in England and Wales, which is used here for UK wide returns data (ICES 2008a) see Fig. 1.4. Model details are given in Box 1.

Box 1. ICES WGNAS PFA model details (ICES 2008a).

The NEAC-PFA model

The WGNAS developed a model to estimate the pre-fishery abundance (PFA) of salmon from countries in the NASCO (North Atlantic Salmon Conservation Organization) North East Atlantic Commission (NEAC) area. PFA in the NEAC area is defined as the number of 1SW recruits on January 1st in the first sea winter. The model estimates the PFA from the catch in numbers of 1SW and MSW salmon in each country. These are raised to take account of minimum and maximum estimates of non-reported catches and exploitation rates of these two sea-age groups. Finally these values are raised to take account of the natural mortality between January 1st in the first sea winter and the mid-point of the respective national fisheries. The Working Group has estimated a natural mortality value of 0.03 (range 0.02–0.04) per month. A Monte Carlo simulation (10,000 trials) using 'Crystal Ball v7.2.1' in Excel is used to estimate confidence limits on the PFA values. Potter et al. (1998) provides full details of the model. Further modifications to improve the model were incorporated during the Working Group meeting in 2005 (ICES 2005).

Overall population trends

The Atlantic salmon has been in decline throughout its range since the 1970s, with particularly strong downward signals since the early 1990s (ICES 2008a), see Fig. 1.4. There has also been a concomitant decline seen in both growth and the relative abundance of MSW fish to grilse in many rivers throughout this time (Jonsson & Jonsson 2004a; Quinn et al. 2006).

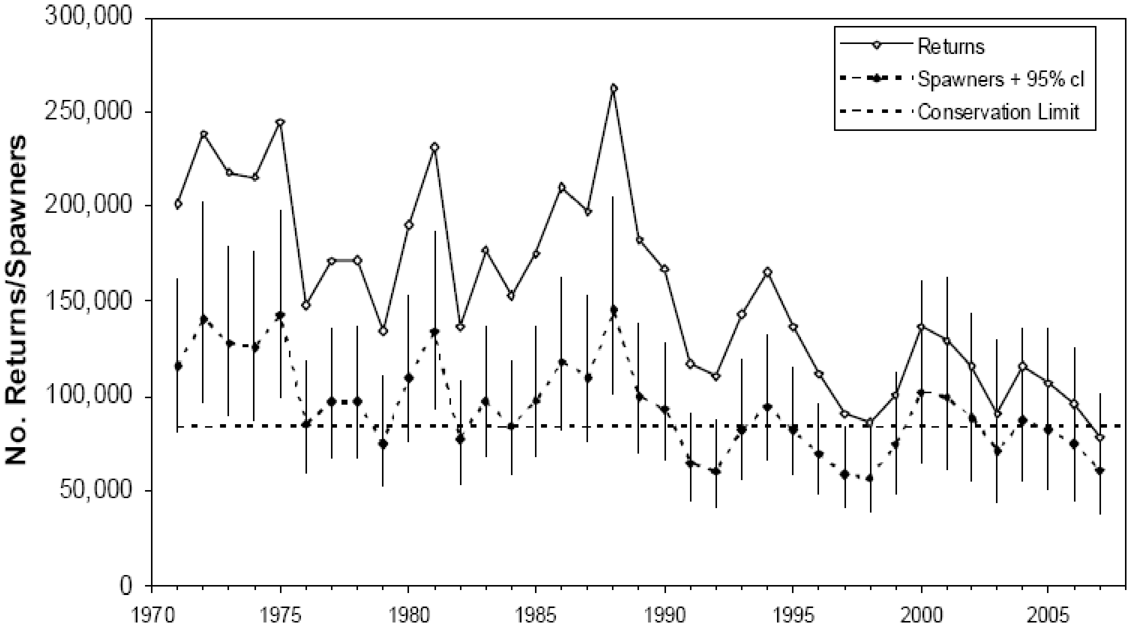


Figure 1.4. ICES pre-fishery abundance (PFA) model estimates of Atlantic salmon in England and Wales, 1970 – 2007 (ICES 2008a).

1.3 Proposed explanations for population patterns

Freshwater problems

As mentioned briefly above, reduction in habitat, pollution, silting, temperature changes and acidification have all had impacts on the freshwater stages of Atlantic salmon populations. Insufficient suitable habitat for juvenile territories leads to poor early life growth and survival, while spawning habitat loss through damming, siltation, pollution and disturbance results in lower initial potential population (Cowx & Van Zyll De Jong 2004). Temperature changes, linked to the North Atlantic Oscillation (NAO), are correlated strongly with juvenile survival to smolt production (Boylan & Adams 2006), due to energetic costs and respiratory rate increases linked to higher temperatures (Elliott 1991; Jonsson & Jonsson 2005).

Smolting and immediate post-smolt

It is commonly thought that the majority of marine mortality, and therefore the largest reason for non-recruitment to the breeding stock, occurs in the first few post-smolt months at sea (Friedland 1998; Friedland & Reddin 2000; Holm et al. 2003; Turrell & Shelton 1993). There are several hypotheses for why this early post-smolt mortality is held to be so important, including possible climatic links to population abundance via primary production, meaning that appropriate prey items may be scarce under adverse climatic conditions (Anderson 1997; Koslow et al. 2002). In years of lower temperatures, for example, salmon smolts may delay entry to the sea, and therefore miss the optimal window of food availability (Kennedy & Crozier 2010; Mills 2003). Alternatively, in years of high primary production, greater availability of prey items may attract predator species, thereby increasing the risk of predation, which is thought to be predominantly size-mediated during the initial marine months (Anderson 1997; Friedland & Reddin 2000; Hansen et al. 2003; Holm et al. 2003). These effects may either cancel each other out, or prey availability may prove to be more important (Stefansson et al. 2003). Later in post-smolt life history, as the post-smolts grow and migrate to common nursery and feeding grounds, there is conventionally thought to be considerably more spatial overlap between the different stocks (Holm et al. 2003). In the northwest Atlantic, the Labrador Sea is thought to be a nursery ground for all North American Atlantic salmon stocks (Friedland & Reddin 2000), while *S. salar* is thought to utilise the Norwegian Sea to the north of the Faeroes for this purpose in the northeast Atlantic (Hansen & Jacobsen 2003), see Fig. 1.5. Despite this relative aggregation, the complexity of nursery habitat is considered to be such that ocean climate and fishing pressures may, respectively, be too broad and fine scale to prove good indices of salmonid abundance (Friedland & Reddin 2000).

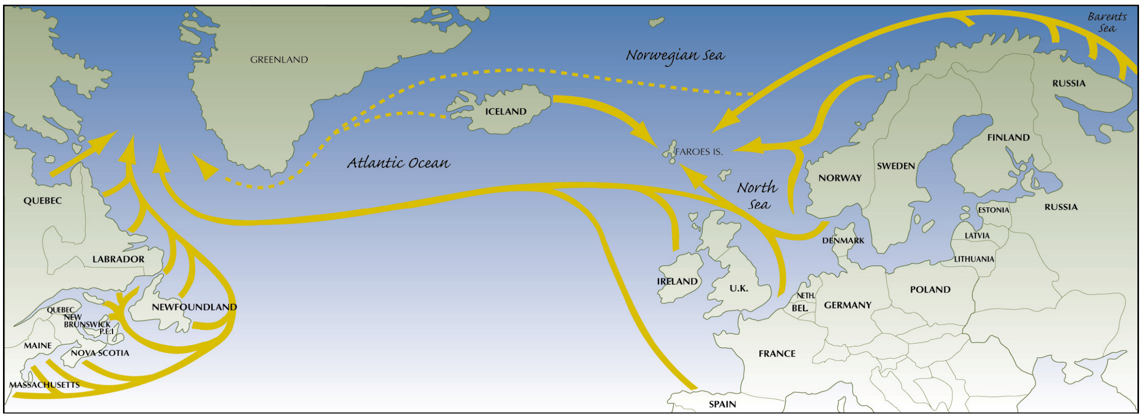


Figure 1.5. Map of proposed wild Atlantic salmon migration in North Atlantic (Atlantic Salmon Federation 1997-2007).

Marine problems

Fishing

Anthropogenic mortality via direct or indirect exploitation is unlikely to be a strong causative factor in the overall population decline of *S. salar*. This is particularly true at the early post-smolt stage when the stocks are generally spatially discrete, affected by regional rather than broad scale phenomena, and unlikely to exhibit synchronous declines (Friedland & Reddin 2000). Friedland and Reddin (2000) suggest that a spatial scale of c.500km is the smallest unit for synchronous influence of a particular oceanic variable over an entire marine fish population, due to the vast area of habitat available over which a variable may be affecting a migratory species such as the salmon, see Fig. 1.2. Fishing is highly unlikely to cause synchronous decline at this large spatial scale. It is also unlikely that fishing is playing a major part in the continued recent decline, as many commercial fisheries have been bought out by government conservation initiatives, including the North Sea Driftnet fishery and many other previously important commercial fisheries around the UK (ICES 2008a). Despite the closures of driftnet, trammel net and other coastal fisheries, which had the greatest impact on stocks when salmon were concentrated at the coast on return migration, overall positive patterns trends in stocks have not been observed (Dempson et al. 2004).

Farming

One potentially significant impact on Atlantic salmon mortality is the presence of large scale, industrial salmonid aquaculture within the migration habitat of wild stocks. Salmon farming may impact on wild populations through unintentional releases of cultured fish, environmental deterioration, overfishing of prey species and spread of associated parasites and diseases (Bakke & Harris 1997; Noakes et al. 2000). The specialisation of salmonids to their natal catchment means that introgressions by non-native farm escapees and hatchery introductions may cause out-breeding depression (McGinnity et al. 2007), particularly due to the greater success in mate competition of domesticated strains of *S. salar* conferred by their larger size and increased aggression (Bjornsson & Bradley 2007; Hansen & Jacobsen 2003; Metcalfe et al. 2003; Saunders 1991). In addition, the concentrations of disease and parasites in cultured salmon cause severe deleterious effects on wild stocks on coming into contact with escaped farmed fish (Bakke & Harris 1997; Saunders 1991). Unfortunately, however, gauging the impact of domesticated salmon on the wild Atlantic salmon is beyond the scope of this research.

Climate

NAO and similar cyclical features

Jonsson and Jonsson (2004b) showed a link between post-smolt growth and maturation and the North Atlantic Oscillation Index (NAOI). The North Atlantic Oscillation (NAO) refers to changes in pressure between a region of low pressure over Iceland and a region of high pressure over the Azores, with the difference recorded as the NAOI. The positive phase of the NAOI, where the pressure difference is greater, is associated with stronger westerly winds across the North Atlantic, leading to warmer, wetter winters in Europe. Negative phases of NAOI result in weaker westerlies, with Europe experiencing cooler, drier winters (Hurrell et al. 2003).

Winter NAOI values have generally increased over recent years; see Fig. 1.6, leading to increasingly warm temperatures in the North Atlantic in winter. A negative relationship between northern hemisphere temperature anomalies and salmon catch rates in some northeast Atlantic countries' home waters has been shown (Beaugrand & Reid 2003; Peyronnet et al. 2008). The effects of these changes on salmon are discussed in the following section. The NAO, however, does not appear to exert a strong, controlling influence on many salmon stocks, possibly because the scale at which it is influential is very broad, meaning that the NAOI might directly explain only a small proportion of the variation in any individual stock (Beaugrand et al. 2003; Beaugrand & Reid 2003; Brander & Mohn 2004; Peyronnet et al. 2008).

In the marine environment, it is unclear how precisely the issues discussed above affect different salmon populations. If all UK salmon feed in a mixed location at sea, it is logical that they would be affected in similar ways by marine problems. If, however, salmon populations and cohorts therein use separate areas of the North Atlantic as feeding grounds, they would logically be affected in different ways by pressures incident on them within their feeding grounds. It is therefore imperative to the effective conservation and management of stocks that the location of salmon feeding grounds at sea are known in order to understand and mitigate threats to their abundance within these feeding areas.

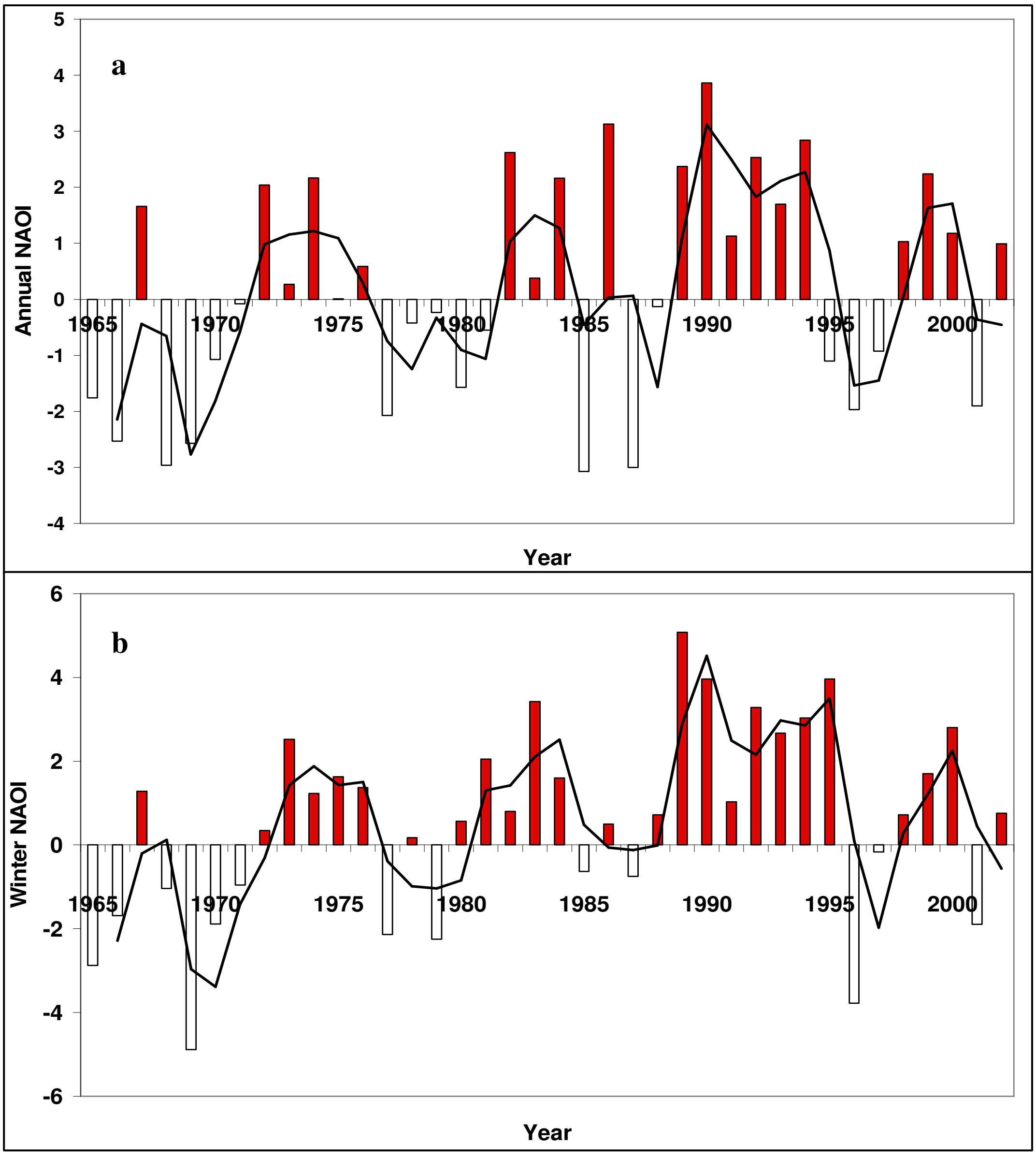


Figure 1.6.a) Annual NAOI and b) winter (December, January, February & March) NAOI, both with smoother line, from 1965 to 2002, showing increasingly positive phase throughout this time (data from Hurrell 1995; Hurrell et al. 2003).

Biology of temperature effects on salmon

Because of shallow habitat use, sea surface temperature (SST) may be used as an index of environmental variability relating to salmon (Peyronnet et al. 2008; Turrell & Shelton 1993). Temperature appears to exert a strong influence on return rates and marine life history strategies for the Atlantic salmon. As mentioned above, return rates have been strongly correlated with winter NAOI (wNAOI) (Boylan & Adams 2006; Peyronnet et al. 2008), and thus SST (Jonsson & Jonsson 2004a; Jonsson & Jonsson 2004b). It has also been observed that survival and returns of grilse are positively correlated with the extent of sea area in the North Atlantic with SST between 8 and 10ºC around May, when smolts first enter the sea from freshwater, and negatively correlated with the area of 5 to 7ºC SST, where salmon exhibit lower swimming speeds (Friedland et al. 2000; Hansen et al. 2003; Montevecchi & Cairns 2003; Reddin & Friedland 1993). In colder years, phytoplankton blooms may be delayed, leading to delays in zooplankton population growth and nutritional stress for the outgoing smolts, or the entry of smolts to the sea may be delayed due to acclimation stress (Mills 2003). In warmer years, however, as seen recently with increased NAOI and warming at the southern reaches of the Atlantic salmon range (Hughes & Turrell 2003), the range and abundance of common prey items such as euphausiids and the large cold water copepod *C. finmarchicus* has declined. Correspondingly, there have been increases in the range of smaller, warm water copepods, linked to higher winter NAOI, which are less favourable post-smolt prey items and occur later in the year, which, combined with increased energetic costs for post-smolts in warmer waters, leads to nutritional stress for salmon (Beaugrand et al. 2003; Beaugrand & Reid 2003; Brander et al. 2003). In particular, *C. helgolandicus* has progressively substituted for *C. finmarchicus*, shifting the peak in *Calanus* abundance from spring to late summer (Beaugrand et al. 2003; Beaugrand & Reid 2003). Combined with the zooplankton changes, removal or delay of feeding aggregations of small fish that prey on *Calanus*, and may also form important prey for *S. salar* (Peyronnet et al. 2008), may create a significant deficit at an important feeding time for post-smolts. The significance of the temperature related effects discussed above is borne out by studies reporting declines in salmon growth over recent decades, concurrently with increases in temperature in the North Atlantic and regime shifts in plankton communities, correlated to the increasing NAOI (Anderson 1997; Beaugrand et al. 2003; Beaugrand & Reid 2003; Brander & Mohn 2004; Friedland 1998; Friedland et al. 1999; Friedland et al. 2000; Jonsson & Jonsson 2004b; Peyronnet et al. 2008; Peyronnet et al. 2007)

Overall, warmer years are associated with faster growth, earlier maturation, and increased lipid over protein storage, resulting in smaller size at return, while in colder years growth is slower, with increased age and size at maturity (Friedland et al. 2000; Jonsson & Jonsson 2004b; Marschall et al. 1998). These influential temperature effects on Atlantic salmon indicate that smolts and post-smolts are highly sensitive to changing oceanic conditions, and have narrow requirements in oceanic conditions to recruit successfully to adult spawning populations.

It has been strongly proposed that marine climate, such as the effects of the NAO, have a strong impact on salmon survival throughout their life history, which is linked to migration patterns both downstream and in the marine environment. In order to test whether these climate-driven changes impact salmon populations, to determine the mechanisms of any such impacts and to assess the nature of such climatic impacts on individual river stocks, the location of marine feeding grounds must be known on a stock-specific level, and long-term data series are required.

1.4. Stable Isotope analysis (SIA) and background

Stable isotope analysis is an excellent technique for studying the ecology of cryptic species, as it is cost-effective, rapid and can investigate higher numbers of ecological interactions than it is often possible to study directly, without observer bias. For a species such as the Atlantic salmon, information on movements and trophic level can be derived without the problems caused by direct observation (Courtemanche et al. 2005; Cunjak et al. 2005; Hutchinson & Trueman 2006).

Stable isotopes are non-radioactive naturally occurring isotopes of elements, which occur in predictable proportions throughout the environment, for example ^{14}N and ^{15}N are stable nitrogen isotopes where ^{15}N occurs at 0.3663 atom % in atmospheric N_2, with the remainder made up by ^{14}N (Högberg 1997). Stable isotope ratios are expressed in δ notation as parts per thousand (‰) deviation from the international standards Vienna Pee dee belemnite (carbon) and Air (nitrogen), according to the equation:

$$\delta X = [(\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{standard}}) - 1] \times 1000$$

where X is, for the purposes of this research, ^{15}N or ^{13}C per mil (‰) and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$.

(Courtemanche et al. 2005; Cunjak et al. 2005; Högberg 1997; Hutchinson & Trueman 2006)Natural biochemical reactions at the Earth's surface very rarely proceed to equilibrium, and kinetic isotope fractionation occurs where energetics favour incorporation of the lighter isotope into reaction products. Synthesis of compounds such as ammonia, urea or carbon dioxide results in preferentially excretion of light isotopes, leaving the remaining tissues enriched in the heavy isotope. Tissues thus inherit a heavy isotopic value relative to diet (DeNiro & Epstein 1978, 1981).

In natural systems, isotopic enrichment, or tissue-diet spacing (Δ), for a whole organism (bulk tissue) has been measured at a mean value of approximately 3.4 per mil in $\delta^{15}N$ and 1 per mil in $\delta^{13}C$ per trophic level (DeNiro & Epstein 1978, 1981). These values, however, are variable and dependent on a number of different factors; these include taxon, mode of excretion (e.g. ammonotelic, ureotelic etc.), growth rate, tissue type measured, amino acid composition of tissues and diet, diet quality, nutritional status and environment (terrestrial, freshwater or marine) (Högberg 1997; Vanderklift & Ponsard 2003). The greater complexity of converting nitrogenous waste to urea or uric acid, e.g. in mammals, birds and reptiles, from ammonia also leads to greater fractionation in the body, as the more complex processes of excretion generally produce isotopically lighter wastes, leaving the tissues of the organism further enriched in the heavier isotope (Vanderklift & Ponsard 2003). Experimental studies of nitrogen tissue-diet spacing in marine fish typically yield values closer to 2.5 - 3‰. The tissue isotopic composition is in turn dependent on the isotopic compositions at the base of the foodweb, which are controlled by ambient conditions and primary production taxonomy (detailed below). The isotopic composition of primary producers therefore constrains the starting values from which enrichment or depletion of a consumer organism are measured. Measurements of tissue-diet isotopic spacing are weighted averages of the isotopic fractionation during synthesis of each component molecule. As an example of variation in the isotopic fractionation associated with molecular synthesis, McClelland and Montoya (2002) studied variations in $\delta^{15}N$ values for 13 amino acids in plankton, and found ranges of up to 13.6‰ between the most enriched and depleted amino acids in any single tissue. Essential amino acids (EAA) such as phenylalanine (Morris 1991) tend to be conserved between food and consumer, thus maintaining their isotope values, while non-EAAs such as glutamic acid (Morris 1991) may be subject to trans- and de-amination within the consumer, causing fractionation to occur (McClelland & Montoya 2002). This differentiation in isotope values between amino acids also leads to tissue- and taxon-specific differences in tissue-diet fractionation factors, as different tissues, and potentially taxa, have differing amino acid compositions, and different taxa may have differing capabilities for molecular synthesis. Isotope values of different taxa are also determined by their modes of food intake, excretion, and growth. New World herbivores have different $\delta^{13}C$ values dependent on whether they are grazers or browsers, as the photosynthetic pathways for trees and C4 grasses fractionate carbon in differing ways (Fogel & Cifuentes 1993). Carnivores, omnivores and herbivores would be expected to show isotopic signatures that are significantly different from one another also, due to varying trophic level fractionation effects (Bocherens et al. 1995; Lee-Thorp et al. 1989). Added to all of these effects, growth rate plays a strong role in controlling fractionation within an organism and is dependent on the ratio of efflux to influx of the isotope source (Riebesell et al. 2000). Where nutrient efflux is high relative to influx, for example under nutritional stress or high growth rate relative to available nutrients, there will be greater discrimination against the heavier isotope in a reaction, with the light isotope preferentially incorporated into the reaction products, leaving the tissue relatively enriched in this heavier isotope compared to the diet (Doucett et al. 1999a). Trueman et al. (2005) also found that higher growth rates under optimal nutritional conditions lead to an increase in resource use efficiency, lowered in-situ biosynthesis of non-essential amino acids, and thus lower tissue-diet spacing. Food quality in terms of N:C ratio, which may be used as a proxy for protein content, may also influence fractionation; (Vanderklift & Ponsard 2003) found that a higher N:C ratio resulted in higher values of δ^{15}N, again likely reflecting reduced in-situ biosynthesis of non-essential amino acids. All of these factors contribute to the isotopic signature of an organism, and must be taken into account when using isotope analysis to infer aspects of ecology.

Jennings et al. (2008a; 2008b) reported that in size-structured marine ecosystems nitrogen isotope values vary with body mass rather than taxon, the slope of the relationship between δ^{15}N values and mass indicating the predator-prey mass ratio. Work has been carried out to determine diet-tissue isotopic spacing in salmon, where captive fish were kept under optimal conditions of nutrition, and given feed from the same source throughout their growth. Diet-tissue spacing (Δ_{d-t}) averaged 2.3‰ (±0.3‰) and 0.0‰ (±0.3‰) for N in muscle and liver respectively, 2.1‰ (±0.1‰) and 1.6‰ (±0.3‰) for C, again in muscle and liver respectively (Trueman et al. 2005). These values are different to the values of Δ_{d-t} per trophic level quoted in the literature (DeNiro & Epstein 1978, 1981), which represent average values for a number of different taxa, meaning that organism-specific values of Δ_{d-t} must be taken into account when interpreting trophic fractionation values.

Self-catabolism during periods of nutritional stress, for example during the return spawning migration of the Atlantic salmon, may also lead to enrichment in both ^{13}C and ^{15}N. The expected linear relationship between δ^{13}C and δ^{15}N, based on standard Atlantic salmon trophic level enrichment values, may be used as an index of body condition in terms of nutritional status. Although, it must be noted when using this relationship, grilse use proportionally less of their energy reserves than MSW fish during their homing migration (Doucett et al. 1999a). The catabolism of relatively ^{13}C-depleted lipids and of relatively ^{15}N-enriched proteins as energy sources when under nutritional stress leads to, respectively, light δ^{13}C and heavy δ^{15}N values in the remaining unused tissues (Doucett et al. 1999a), leading to decoupling of the expected linear trophic enrichment of ^{13}C with ^{15}N. The isotopic ratio of δ ^{13}C to δ ^{15}N may therefore be used to infer poor condition on return to natal streams.

Carbon isotope variation in marine ecosystems

There are considerable differences in the isotopic composition of carbon between freshwater and marine ecosystems, and also between inshore and offshore environments (Miller et al. 2008). It has been observed that marine trophic webs are generally more enriched in heavier stable isotopes, including those of carbon and nitrogen, than those of freshwater or terrestrial environments (Boutton 1991; Hobson 1999). Bearhop et al. (1999) found a general ^{13}C enrichment of 7‰ for marine organisms compared to those in freshwater, while Doucett et al. (1999a) observed that marine primary production was in general enriched with the heavier stable isotopes of carbon and nitrogen compared with that of freshwater. In agreement with this, Boutton (1991) demonstrated lower δ^{13}C values in the total dissolved inorganic carbon (DIC) of freshwater compared to marine waters. The principle reason for the c.7‰ offset in the isotopic composition between marine and terrestrial ecosystems is the source of carbon fixed into the food web. On land this is mostly soil-respired carbon dioxide, depleted in ^{13}C (Bahn et al. 2009), while in marine environments DIC, incorporating both dissolved CO_2 and bicarbonate ions, is incorporated into primary production. DIC is enriched in ^{13}C relative to atmospheric CO_2 (Bearhop et al. 1999; Craig 1953; Hutchinson & Trueman 2006; Zhang et al. 1995).

An additional difference in carbon isotope compositions between marine and terrestrial systems arises from the origin of food. Dietary carbon sources may be either allochthonous, from input external to the aquatic system such as leaves etc., or autochthonous, from primary production within the ecosystem (Doucett et al. 1996). In allocthonous systems (generally prevalent in terrestrial aquatic systems) the isotopic composition of aquatic taxa may be decoupled from primary production within the water body, whereas in autochthonous systems (all open marine systems) the isotopic composition of higher taxa is directly linked to associated primary productivity (Eby 2004).

The status of δ^{13}C in a marine ecosystem may be used as a proxy for the characterisation of a water body, as, unlike the more trophically-linked δ^{15}N, it generally reflects the isotopic value of primary productivity at the base of the food chain (Wada et al. 1991a). Carbon isotope variation at sea is strongly related to temperature, as cooler waters contain more dissolved nutrients, including CO_2, leading to greater preferential uptake of the lighter isotope, e.g. ^{12}C, whereas there is less available e.g. CO_2 in warmer waters (Lynch-Stieglitz et al. 1995), meaning that phytoplankton bloom values become enriched with the heavier isotopes under these nutrient limited conditions (Hofmann et al. 2000; Kamykowski & Zentara 2005). Temperature also controls growth rate (μ), see Fig. 1.7, whereby plankton cells tend to grow faster under warmer conditions (Hofmann et al. 2000), and thus exhibit less preferential uptake of the lighter isotope, taking in all available nutrient sources in order to maintain their growth at high rates (Kukert & Riebesell 1998; Laws et al. 1995; Riebesell et al. 2000; Trueman & Moore 2007).

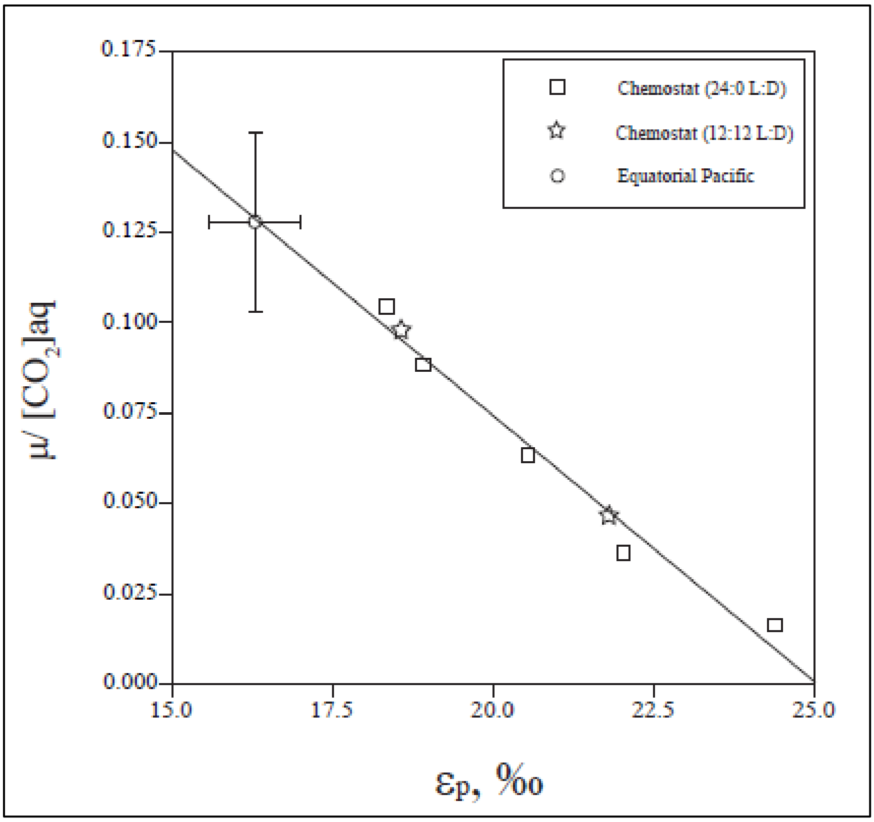


Figure 1.7. “Relationship between μ/[CO]aq and ε_p (the biological fractionation associated with carbon fixation) for *Phaeodactylum tricomutum* grown in a chemo(cyclo)stat system under light:dark (L:D) cycles of 24h:0h and 12h:l2h (modified from Laws et al. 1995). The open circle is the mean of the range of reported growth rates (0.585 d^{-1}) in the equatorial Pacific multiplied by 2.35 to correct for L:D cycle and respiration effects and divided by the [CO]aq of 10.8 μmol kg^{-1}. The corresponding ε_p is 16.3‰”. Error bars are ±1SD (modified from Laws et al. 1995).

The combination of lower nutrient resource availability and higher growth rate under warmer temperatures leads, therefore, to enrichment in ^{13}C. This is often reported as a latitudinal gradient in $\delta^{13}C$, see Fig. 1.8, with lower, warmer latitudes having more enriched phytoplankton ^{13}C (Lorrain et al. 2009).

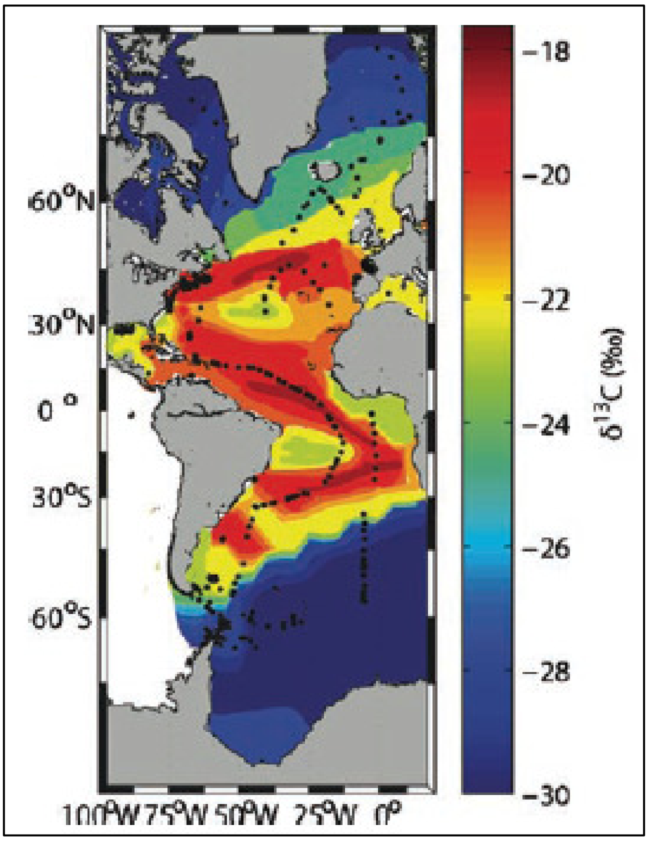


Figure 1.8. Contour plot of isotope values in the Atlantic Ocean based on published data (after Graham et al. 2010).

With higher sea surface temperatures, and as a phytoplankton bloom progresses, enrichment in ^{13}C will occur according to the mechanisms mentioned above, thus a strong bloom that has been productive for a long time in warm conditions would be expected to contain organic carbon that is considerably enriched in ^{13}C compared to a smaller, shorter bloom in cooler conditions (Fry 2006; Hofmann et al. 2000; Trueman & Moore 2007), and the isotopic signature of the bloom would subsequently be propagated up the trophic web.

Species composition of primary producers is also important in determining isotopic values. As a bloom advances and phytoplankton cells decay, ammonium becomes a major source of nitrogen. Certain enzymes important in ammonium uptake (e.g.), phosphoenol carboxykinase (PEPCK) and phosphoenolpyruvate carboxylase (PEPC), are associated with decreased isotopic discrimination and therefore cause relatively enriched levels of ^{13}C in diatoms (PEPCK only) and dinoflagellates (PEPC & PEPCK) (Lara et al. 2010). This likely inundates the cells with undiscriminated carbon ions, as opposed to Rubisco, which they also contain but which is more discriminatory in its isotopic uptake. Diatoms are also fast-growing comparative to many other phytoplankton, which has been found to increase isotopic enrichment through greater efficiency in the use of source nutrients. Hence, locally elevated values of $\delta^{13}C$ through the trophic web may indicate either prevalence of diatoms in the phytoplankton, or rapid primary production incorporating all available isotopes of carbon, rather than preferentially incorporating ^{12}C in a manner common to slower rates of production (Wainright et al. 1993).

These various factors contributing to variation in aquatic $\delta^{13}C$ values mean that there should be clearly observable changes in organism $\delta^{13}C$ values corresponding to changes in feeding location between freshwater, coastal and offshore regions (Miller et al. 2008; Satterfield & Finney 2002). There should also be observable changes between areas of high and low productivity and temperature, as areas where temperature and productivity are high are positively correlated with more positive $\delta^{13}C$ values. It should also be possible to determine areas of high and low variation in $\delta^{13}C$ through time.

Nitrogen isotope variation in marine ecosystems

Similar to carbon, $\delta^{15}N$ values in dissolved inorganic nitrogen (DIN) increase with decreasing nitrate concentrations, because the phytoplankton preferentially take up $^{14}NO_3^-$. As the lighter isotope is depleted, the phytoplankton then take up $^{15}NO_3^-$, and pass their elevated $\delta^{15}N$ values up the foodweb, leaving the whole trophic chain enriched in the heavier isotope with high primary productivity (Satterfield & Finney 2002; Wainright et al. 1993). Nitrogenous nutrient concentration in the oceans is also temperature dependent, as higher temperatures are linked to lower dissolved nutrient concentrations, leading to reduced fractionation and heavier $\delta^{15}N$ values, according to the mechanism described above (Switzer et al. 2003), but concentrations are also strongly affected by coastal proximity and land use, pollution and trophic level effects (Cabana & Rasmussen 1996; Cole et al. 2004), which makes the basal $\delta^{15}N$ value of a marine food web much harder to establish and interpret than that of $\delta^{13}C$. Other factors affecting the basal signature of primary production, and thus the isotopic values of the whole food web, include the size and timing of phytoplankton blooms, as enrichment occurs progressively through consumption of available nutrients (Fry 2006), remineralisation and upwelling of the lighter isotopes, terrestrial runoff, and atmospheric input (Miller et al. 2008; Trueman & Moore 2007; Waser et al. 2000).

Base values of $\delta^{15}N$ do not differ significantly between pristine marine and freshwater environments (Vanderklift & Ponsard 2003), but freshwater systems impacted by anthropogenic nitrogen sources are typically greatly enriched in ^{15}N

(McClelland et al. 1997) and this enrichment leads to marked coastal-offshore gradients in $\delta^{15}N$ values (Jennings et al. 2008a; Jennings & Warr 2003). In open pelagic ecosystems without strong anthropogenic input, however, the magnitude of variation in $\delta^{15}N$ values caused by bloom size or taxonomic differences in phytoplankton is considerably smaller than that caused by trophic level effects (c. 4‰ per trophic level, DeNiro & Epstein 1981). Marine food chains are typically longer than their terrestrial equivalents, and consequently upper trophic levels in marine ecosystems show the highest $\delta^{15}N$ values (Wada et al. 1991a). The variation observed in $\delta^{15}N$, therefore, is largely caused by, and used to track, trophic level fractionation and status (Jennings et al. 2008a; Wada et al. 1991a).

Isotope summary

In summary, $\delta^{13}C$ values vary dynamically with changes in primary productivity and, as production is spatially variable, they also contain biological information relating to the state of primary production and spatio-temporal information relating to the area of ocean in which the particular production conditions were experienced. $\delta^{15}N$ values, in contrast, relate to both the trophic level of the fish and the baseline $\delta^{15}N$ conditions. A temporal history of primary production conditions, relative trophic level and marine feeding area for Atlantic salmon may therefore be constructed retrospectively from $\delta^{13}C$ and $\delta^{15}N$ stable isotope values contained in the collagen of archived scales.

1.5. Fish scales as a substrate for stable isotope analyses

Scale morphology, composition and function

Fish scales were classified by Louis Agassiz in 1834 into four types: ctenoid, cycloid, ganoid and placoid (Roberts 1993). Ctenoid scales have thin plates with “discrete, separately ossified spines in the posterior field”, and are layers of collagen covered with bio-apatite; cycloid scales again have thin collagen plates under a bio-apatite layer but a smooth posterior edge and no spines; ganoid scales have “thick plates of ganoine and bone”, where ganoine is a bony structure beneath the enamel layer referred to here as bone; and placoid scales have “spine-like denticles of enamel and dentine”, and are very similar in structure to teeth, hence often being referred to as dermal denticles (Roberts 1993). Members of the family Salmonidae have cycloid scales. These are embedded in dermal pockets, where the external layer (EL) is first formed and mineralised with bioapatite (calcium phosphate crystals on an irregular network of thin collagen fibrils) then underplated with laminar sheets composed of parallel helical collagen fibres. As the scale grows, further collagen sheets underplate the initial layers in a plywood formation, extending beyond the original basal plate (BP) on all sides (Zylberberg 2004), see Fig. 1.9 (Zylberberg 2004); the overlap is then mineralised with bioapatite crystals that aggregate and merge, which creates the patterns of circuli observed on the EL (Hutchinson & Trueman 2006; Zylberberg 2004). Scale growth rate is thought to be approximately allometric, with positive allometry during rapid growth in the fish, and negative allometry during slower growth; the scale growth rate slows considerably in older fish, showing quite negative allometry as the fish approach asymptotic size (Casselman 1990).

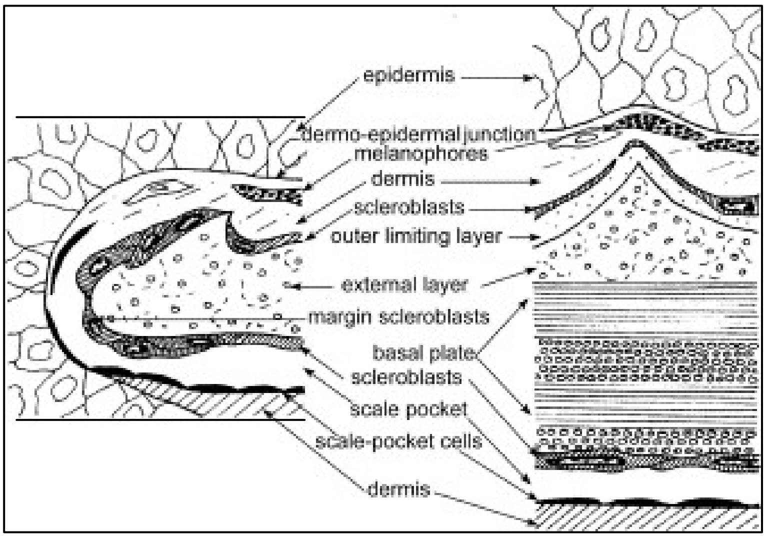


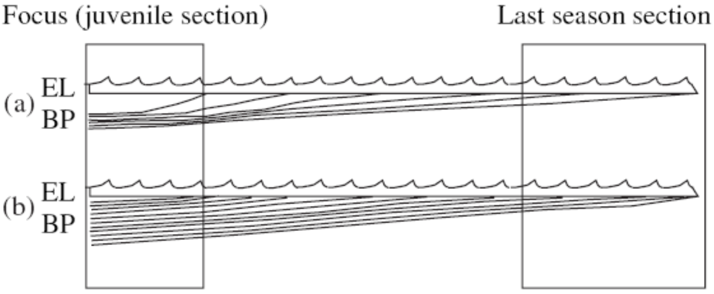
Figure 1.9. Diagram of a section of a typical elasmoid scale in the dermal scale envelope. The section is perpendicular to skin surface (modified from Zylberberg 2004).

The protein, collagen, is a very useful material for the study of biological systems, as it contains both carbon and nitrogen, and incorporates the isotopes of these elements over approximately the same time periods as muscle tissue (Gearing 1991; Satterfield & Finney 2002). Fish scales have been shown to be around 3-4‰ more enriched in ^{13}C and around 0.2‰ in ^{15}N compared to muscle tissue, which reflects a difference in amino acid composition between the two tissue types; scale collagen, for example, contains comparatively more glycine, which is enriched in ^{13}C, than muscle tissue (Satterfield & Finney 2002). Both isotopic offsets increase with fish length, possibly due to the lipid content of muscle for $\delta^{13}C$, and to the high glycine content (depleted in ^{15}N and relatively conserved during assimilation) in scales relative to muscle tissue (Sinnatamby et al. 2008). The strongly positive correlation in isotopic composition of scale collagen and muscle protein for both $\delta^{13}C$ and $\delta^{15}N$(Sinnatamby et al. 2008) makes scale tissue an ideal non-destructive target for isotopic analysis (Perga & Gerdeaux 2003b; Pruell et al. 2003; Satterfield & Finney 2002; Sinnatamby et al. 2008). As collagen is a very complex, long-chain molecule, it is sufficiently metabolically inert that it is not in constant flux and therefore provides a reliable representation of the integrated stable isotope composition of diet during the period of growth. Type 1 collagen (as found in fish scales) is an extremely refractory molecule, and will survive intact for millennia if maintained in a dry, cool environment (Gearing 1991; Holmes et al. 2005; Satterfield & Finney 2002). Fish scales can also be sampled without killing the fish, which is particularly useful for a species of such conservation concern.

The collagen in an Atlantic salmon scale is grown in laminar form, each new layer under plating the previous lamina of collagen as the scale grows outwards, see Fig. 1.10i (Hutchinson & Trueman 2006). This means that a section of scale sampled at the focus would contain isotopic signals from the entire life history of the fish, while a sample taken from the last season of growth will contain only the isotope values integrated to the collagen within that season. The scales have bio-apatite circuli deposited at measurable temporal intervals on the surface of the scale, easily seen under a low-magnification light microscope.

In the Atlantic salmon, circuli are laid down at roughly weekly intervals during the rapid summer growth season, with winter circuli at about half of this rate or less when temperatures are lower and prey is less readily available, so growth is slower (Friedland et al. 1999; Friedland & Reddin 2000; Trueman & Moore 2007). This visible temporal record allows identification and analysis of specific portions of time spent at sea, recorded within the scales over the full period of an archive scale collection. Thus scales may be read and the last season of growth reasonably accurately dissected out for analysis, see Fig. 1.7ii (Hutchinson & Trueman 2006). (1999; 2000)Archived scale collections, which are often held from routine sampling of returning salmon (Davidson & Hazlewood 2005), are ideal for assessment of long-term population trends, as they contain information on age and growth (Jennings et al. 2001a), together with chemical records of diet and movements in the stable isotopes of carbon and nitrogen.

i)



ii)

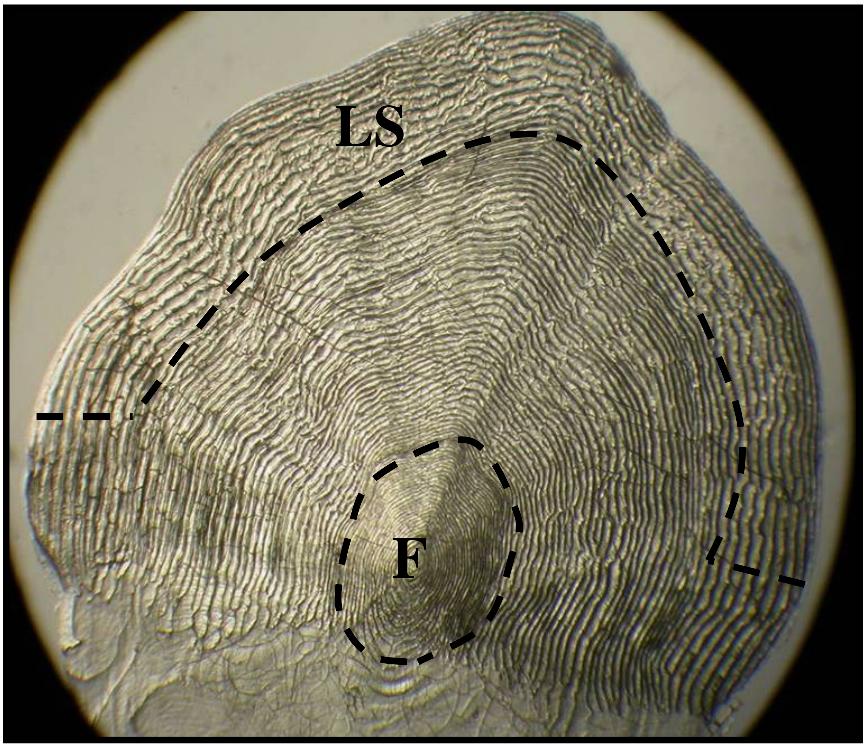


Figure 1.10. i) Hypothetical schematic vertical sections through the medial axis of Atlantic salmon scales summarising two possible mechanisms of collagen growth resulting in (a) minor and (b) severe mixing of early- and late-formed collagen in vertical scale sections (EL, External Layer consisting of bio-apatite; BP, Basal Plate consisting of collagen layers). And ii) Photomicrograph of a scale from an adult Atlantic salmon grilse recovered on return to the natal river, indicating section removed for isotopic analysis (LS). Note that life-history features are determined from spacing of mineralized ridges (circuli) in the uppermost external layer (F, portion of scale laid down during juvenile freshwater residency; LS, portion of scale laid down during the last season at sea (Hutchinson & Trueman 2006).

1.6. Aims and hypotheses

The research presented in this thesis aims to address some of the unknown factors relating to the marine mortality of Atlantic salmon. Specifically, the aims of the project are as follows:

1. Identify existing Atlantic salmon scale libraries in England and Wales.

2. Determine the most useful archives for analysis based on availability, geographic location and continuous temporal coverage.

3. Refine and improve existing methods to measure stable isotope ratios in salmon scales.

4. Measure the stable isotope composition (C and N) from salmon scales through time in relation to relevant variations in the marine environment.

5. Validate the use of scales as samples for stable isotope analysis

6. Use isotopic data to test hypotheses below relating to salmon ecology at sea

Aims 2 to 6 were dependent upon having a good sample range for both grilse and MSW salmon within each sampled archive. Hypotheses concerning behaviour of salmon at sea were developed from existing literature (see introduction). Specific hypotheses tested in this thesis are:

- There is trophic separation between the smaller grilse cohort and larger MSW cohort in both populations.

- Salmon from different English populations feed in a common area in the season prior to return

- Grilse and MSW salmon from the same natal origin feed in different areas in the season prior to return

- Salmon from English populations share feeding grounds with 1SW fish from Newfoundland

2. Materials and methods

2.1. Materials

Available archives

The first output from this project is a database containing information on archived scale collections held throughout England, Wales and Ireland. This is attached as electronic Appendix A. It has been collated from contact made with relevant government agencies and NGOs throughout England, Wales and Ireland. This database details which organisations and individuals were contacted, their area and/or responsibility, whether a response was received, the details of any response, and any available information on archived scale holdings. In summary, eight rivers were identified that held scale collections: Rivers Avon (Hampshire, England), Bush (Northern Ireland), Dee (North Wales/England border), Frome (Dorset, England), Lune (Lancashire & Cumbria, England), Tamar (Devon/Cornwall border, England), Thames (southern England), and Wye (South Wales/England border), with possibly one extra archive held for the Welsh River Taff. Samples were also held for four less specific areas: the Lough Foyle catchment (Northern Ireland), Poole Bay (Dorset), Tyne and Northumbria, and the English North East Coast in general. Of these collections, only the Bush, Lune, Thanes and Lough Foyle sampling programmes were continuing. Further investigations of available and appropriate archives for sampling were based on the initial information contained in this database. Most archives were not multi-decadal, continuous or regularly sampled, thus only the CEH (Centre for Ecology and Hydrology) River Frome and Cefas (Centre for Environment, Fisheries and Aquaculture Science) Northeast Coast Driftnet archives were selected for use in this study.

Problems obtaining samples

Despite scale samples routinely being taken from salmon for ageing purposes for many decades on most salmon rivers, many of these potential archives of scales have been lost or disposed of, several relatively recently. These lost archives include many years of the River Bush, Wye and Dee archives, and almost all from the River Severn (2005), together with various other unidentified rivers anecdotally mentioned as discarded, including many from Marine Scotland, where scale prints are made in acetate before the scales are thrown away. This loss of these invaluable samples has made it very difficult to find long time series of Atlantic salmon scales for comparative analysis. Emphasis must thus be placed on the necessity of retaining tissue archives when in contact with all fish monitoring and sampling bodies.

Scale collections analysed

The scale collections analysed and in progress are drawn from two separate locations in England, the River Frome (CEH, River Frome archive) in Dorset and the northeast English coast (Cefas, North Sea Driftnet archive). These sample archives were kindly provided by the organisations listed above in parentheses. The reasons for selection of these archives are:

- Firstly, availability of longer time-series of samples dictates which areas may be used for analyses,
- Secondly, the geographic isolation between archive population collections means that isotope patterns occurring in the marine phase of life history will enable any differences in marine conditions experienced in terms of temperature, productivity and variability, and potential population feeding areas and therefore migration pathways to be revealed.
- Finally, the routes taken by smolts from these two regions will likely differ significantly due to their geographic separation and entry into marine systems with differing current patterns, see Fig. 1.3.

The use of these archives, representing the northeast and the south of England, enables us to build up a large part of the picture of salmon marine life history around England.

On receipt of each archive, a database was built to contain all information regarding each fish sample included. These databases are in Microsoft® Excel spreadsheets attached as electronic Appendices B and C. Each sample contained in each archive was given a unique ID number to enable later tracking of the samples and their measurements.

River Frome

The River Frome extends from Evershot on the Dorset – Somerset border, to Poole Harbour, at a latitude of 50.5°N, extending for a total distance of c. 70km, comprising a wetted area available to salmon of 876km^2 (ICES 2002; Riley et al. 2009). The River Frome arises in Upper Greensand and Gault Clay, then flows through Chalk and finally Tertiary gravel and sand (Cannan & Armitage 1999). It is dominated by groundwater input, which arises from the Greensand/Chalk and Chalk/Palaeogene boundaries, and the Oakdale Clay Member geology (Arnott et al. 2009). This river is ecologically characteristic of a chalk stream, in that it is highly productive with a large volume of macrophytes, and is predominantly groundwater fed, thus has relatively stable flow and temperature regimes (Berrie 1992; Mackey & Berrie 1991). The favourable conditions of stable flow and temperature, and high levels of macrophyte cover support large populations of fish (Mann 1971). These chalk streams were once, due to their aesthetic value and prolific salmon production, amongst the most valuable for salmon fishing in Britain, and are still very valuable for recreation, the local economy, and the environment (Welton et al. 1999).

The Frome has various problems affecting its native salmon population, including increasing suspended sediment concentrations from surrounding agriculture (Collins & Walling 2007), where arable cultivation dominates the catchment land-use (Casey et al. 1993), and from treated effluent discharged from the Dorchester sewage treatment works (Bowes et al. 2005). This increased sediment load, with its frequent high nutrient concentrations, have been found to negatively impact egg-to-fry survival rates by lessening the amount of dissolved oxygen available to the developing salmon and by physically blocking interstitial gravel emergence space (Hendry & Cragg-Hine 2003; Hilton et al. 2001; Thibodeaux & Boyle 1987). Unlike other major UK chalk streams, however, the Frome has not been affected by genetic dilution from the stocking of reared fish (Welton et al. 1999). Biological oxygen demand may be increased for organisms in the Frome, as chalk streams across the south of England have experienced concurrent rises in water temperature over at least the last two decades for which measurement data exist (Durance & Ormerod 2009). It is thought that temperature rises may be a causative factor in the decline of Frome salmon, with years of notably low flow, e.g. 1989-1992, and increased metabolic demands, both implicated as causes of reductions in numbers of out-migrating smolts and returning adults (Welton et al. 1999)

Historically, the Frome has been well-monitored for salmon, with an electronic resistivity fish counter in operation since 1970, providing the longest dataset for salmon migration in the UK (Welton et al. 1999). The data from this counter has shown that returning adult numbers dropped precipitously between the late 1980s to early 1990s. CEH has carried out an ongoing sampling programme on returning salmon concurrently with the operation of the counter, which has found that an increasingly large proportion of the returning fish made up of grilse; this cohort has declined in size through the monitoring period (ICES 2009b). The sampling programme and counter are now run by the Game and Wildlife Conservation Trust (GWCT), which took over the East Stoke Research Station in 2009. The archived scale samples used are taken from the collection owned and collected by CEH. These samples span the period 1971 to 2002 inclusive, and each has information on date of capture, size of fish in length, mass or both, together with any additional information that may have been recorded at time of capture or during subsequent examination of the samples. These archived samples were cleaned and mounted on labelled glass microscope slides for ease of reading by CEH. For analysis, they were photographed on the slide mounts before being removed, cleaned further and dissected. To date, 324 individual fish (183 grilse and 141 MSW) have been analysed from this archive.

Northeast Coast

The Northeast Coast scale collection comes from an archive of samples taken while a driftnet fishery was in full operation along the northeast English coast, harvesting salmon from the River Coquet, through the Tyne, Wear, Tees, as far as the Yorkshire Esk to the south, and from adjacent Scottish rivers to the north, see Fig. 2.1. Unlike the Frome, none of the rivers thought to be represented by this archive are ICES North East Atlantic Commission (NEAC) Index Rivers, thus are not as well monitored and researched for their salmon populations (ICES 2002). This fishery was the largest net fishery in the UK until 2003, when a phased buyout was initiated through the Department for Environment, Food and Rural Affairs (Defra) due to dwindling stocks; this meant that only 16 net licenses were held for this fishery between 2003 and 2007, compared with 69 in 2002 (Anon. 2007). This northeast region has been, and continues to be, the source of the majority of salmon catches in England and Wales since the late 1960s, comprising 91% of the total northeast coast salmon catch between 1998 and 2002 (Anon. 2005b), with the River Tyne having the highest rod catch of salmon for any river of England and Wales in 2001 (Mawle & Milner 2003).

The rivers this archive is thought to represent have suffered from the heavy industrialisation and population increase in the northeast region over the last century, particularly in the early to mid-1900s (Anon. 2004). This industrialisation led to reductions in water quality due to effluent and runoff entering the rivers from sewerage works, mines and factories in the catchments, together with changes in land use and river management (Anon. 2005a). The disturbances and water quality reductions in these rivers caused declines in salmonid abundance, particularly along the reaches of the River Tyne, which is currently the largest and most prolific salmon river in the northeast of England (Anon. 2005b). Due to the Tyne's status as the most productive river represented by this archive (see Table 2.1 for details), it will be used here as an example of the ecological conditions experienced by the salmon caught in the driftnet fishery.

Table 2.1. Northeast and River Tyne reported rod catch, 1995-2002 (Anon. 2005b).

Year	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**
Northeast rod catch (no.)	2201	2514	2445	2941	2670	3600	3733	3967
Tyne rod catch (no.)	1236	1667	1460	1808	1898	2297	2513	2585
Tyne rod catch (%)	56.2	66.3	59.7	61.5	71.1	63.8	67.1	65.2

The Tyne begins as two separate rivers, the North Tyne which flows off Peel and Deadwater Fells, and the South Tyne which rises near Cross Fell; these rivers then flow eastward to join at, appropriately, Watersmeet and continue as the River Tyne to meet the North Sea at Tynemouth. This river is at a latitude of 55°N, extending for a total distance of c. 321km, comprising a catchment surface area of approximately 2933km^2 (ICES 2002). The underlying geology of this region is largely Carboniferous Limestone, Millstone Grit, Devonian and Old Red Sandstone, and Coal Measures, with some small areas of overlying peat and boulder clay deposits (Williams et al. 2009; Williams et al. 2008a; Williams et al. 2008b; Williams et al. 2008c). Land use in the upper catchment is largely agricultural, with most of the North Tyne flowing through the Northumberland National Park, where water quality is typically very good (Williams et al. 2008a). From an historic high rod catch of more than 3000 salmon in 1927, the Tyne salmon population declined throughout the mid-20th century until it was declared "biologically dead" in 1957, following a year of no rod catches (Anon. 2010). This is thought to be principally due to industrial and domestic pollutant discharge directly into the river from the heavily urbanised and developed Lower Tyne Valley, where industries such as ship building and mining contributed to poor water quality, together with a large volume of sewage from the populace (Mawle & Milner 2003; Williams et al. 2008a). Following the decline of industry and the improvement of the Tyneside sewage works in the 1960s, salmon began returning to the catchment, likely both from a remnant river stock and from returning fish straying from nearby rivers (Anon. 2004). With the construction of the Kielder dam and reservoir, which completed in 1979, and the resultant loss in spawning and juvenile habitat, Northumbrian water was legally obliged to provide mitigation measures, which came in the form of Kielder hatchery, which has stocked out at least 160,000 juvenile fish annually, and usually considerably more, since 1979 (Williams et al. 2008a). While this has undoubtedly contributed to the continued increase in Tyne salmon, it is thought that water quality improvement is by far the most important factor (Milner et al. 2004). River management measures such as Kielder Dam also regulate flow in the downstream catchment, meaning that problems with summer low flows and increased temperature are largely removed, although there are many anthropogenic barriers to salmon migration. A significant amount of water from the Tyne is used for hydroelectric power generation, along with abstraction to neighbouring rivers, including the Derwent, Tees and Wear, both of which factors contribute to the removal of natural salmon habitat (Anon. 2004; Williams et al. 2008a). The pollution and habitat alteration or removal issues faced by salmon in the River Tyne are typical of rivers from the northeast coast of the UK and of southeast Scotland, where all have faced threats from poor water quality and urbanisation over the past century, but have similarly recovered with habitat and population management measures, bucking the national trend towards salmon decline

Cefas hold archived samples from 1985 to 2001 for the Northeast Coast Fishery, from which our samples are taken. These samples are labelled with information on the date of capture and size of the fish, again in length, weight or both, together with any additional information held by Cefas. The scales are uncleaned, and in the original annotated scale sample envelopes to which they were transferred at time of sampling. All available fish, totalling 289 individuals (152 grilse and 137 MSW), have been analysed from this archive.

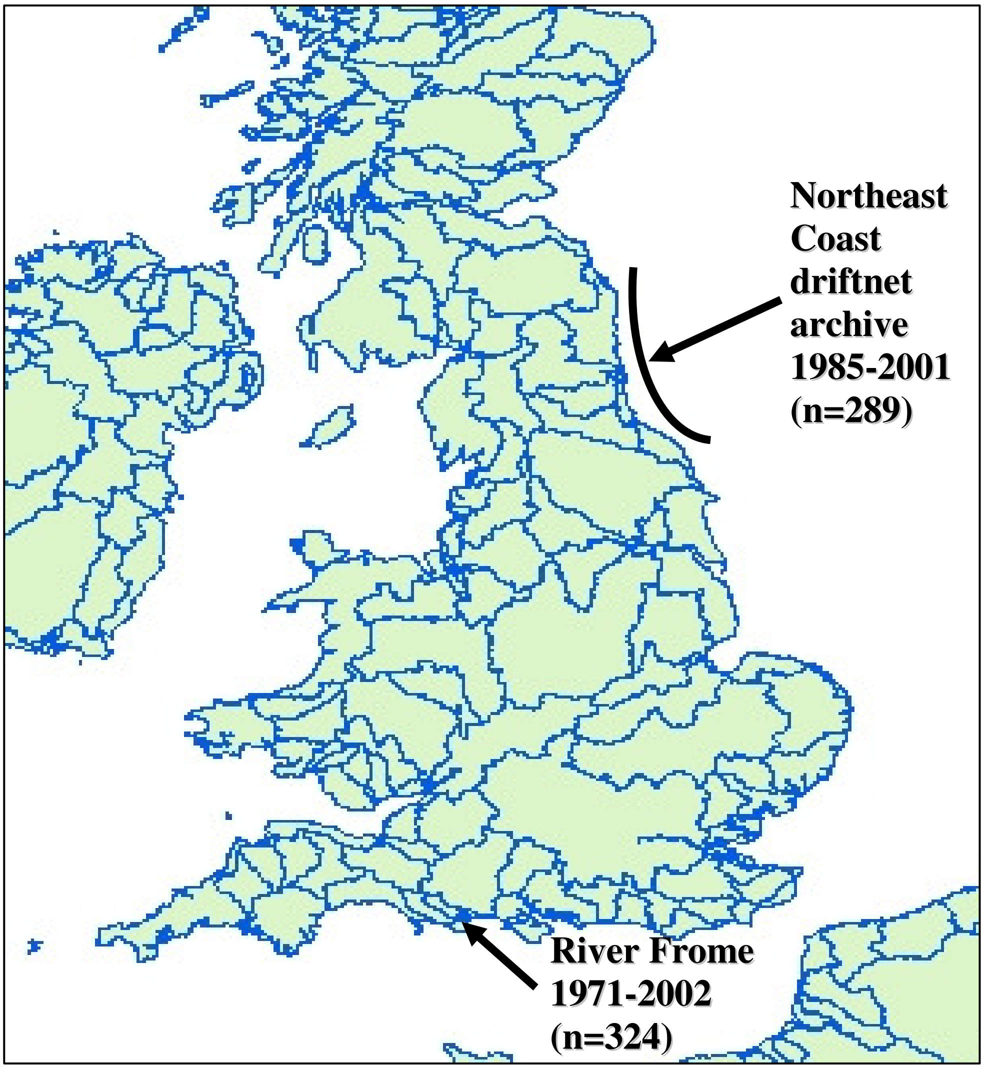


Figure 2.1. Map showing the locations of rivers from which archived scale samples have been taken for this project (after Anon. 2001).

The two populations chosen for study are serendipitously the best archives available for the period represented by this study and have excellent contrasting geographic representation of significant salmon populations in England.

2.2. Methods

Scale samples and dissection protocol

The first step in refinement of analytical technique was to standardise the dissection protocol for all scale samples, dependent on the age of the fish as read from the scale. Age was classified according to the internationally-recognised system where freshwater age is recorded first, then marine age. The full salmon year runs from the beginning of April until the end of March. So, for example, a fish leaving freshwater after one year only, as defined by the location of the smolt line, and then captured on return to freshwater in March (a year after leaving) would be recorded as 1.1. If plus growth, i.e. growth beyond the recorded full year but less than another full year, is seen, or if the fish is captured after March, whether it has visible plus growth or not, each number would be recorded as e.g. 1+1+. This convention is followed for as many years as may be read on the fish scales. The summer and winter portions are determined by the proximity of the circuli to one another, where the scales, and the fish, grow slowly under the resource-limited conditions of winter meaning that the winter circuli are closely spaced, appearing as a dark band on the scale, while the summer circuli are more widely spaced, reflecting the better feeding and growth conditions, and appear as a light band, see Fig. 2.2.

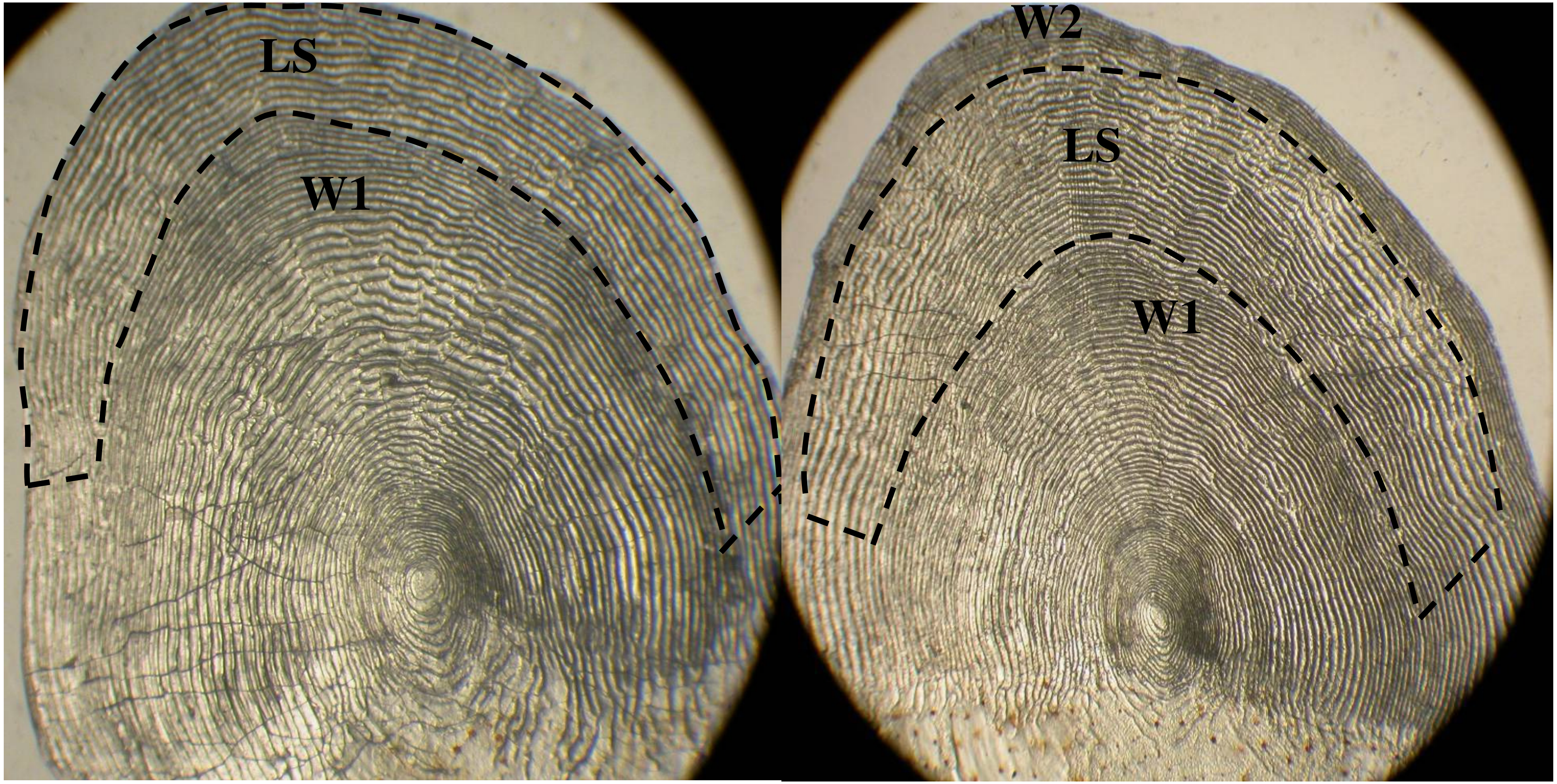
Scales from fish that had spawned previously to their return and capture point (kelts) were excluded from analysis, as their scales showed signs of resorption, making it very difficult to determine the area of growth for the last full season at sea. Example kelt scales are shown in Fig. 2.3, where 2.3.a. is a kelt that spawned immediately prior to capture and has resorbed much of the last season of scale growth, and 2.3.b. is a kelt, that has spawned in the previous year to that of capture. This resorption leaves a line known as a spawning mark after regrowth of scale material, and is caused by nutritional stress from maturation and the return spawning migration, when the mature salmon have ceased to feed (ICES 1992; Richard & Bagliniere 1990; Stokloso 1970).

On discussion with Cefas' scale reading specialist, Bill Riley, it was determined that the outer last season of growth should be dissected from grilse, as shown in Fig. 2.2 a. From MSW fish the last full season of growth should be dissected, as shown in Fig. 2.2 b. This ensures that a similar and consistent portion of marine growth is analysed for every fish, meaning that results will be comparable. This method contrasts to that of Sinnatamby et al, (2009; 2008), in which the entire marine portion of the scale was used for analyses; however preliminary experiments demonstrated that there are differences in isotope values between whole marine portion and last season of growth in scales (Trueman, unpubl. data). This is logical in accordance with the laminar growth of the collagen layers, i.e. the whole marine portion would give a signal biased towards the later collagen layers, with some potential late freshwater influence, while the last season of growth would give a clear signal integrated over that portion of growth alone (Hutchinson & Trueman 2006). It was determined that the best place to obtain a clear reading from a scale is at the base where the circuli terminate at the external portion (Bill Riley, pers. comm.), where the seasonal bands of circuli tend to be the clearest. Using this method, all scales used could accurately be read, and the end circuli of each season followed to obtain an accurate dissection.

Each sample was photographed prior to dissection using a Nikon Coolpix camera mounted onto a Wild binocular dissecting microscope with transmitted light. These photographic records enable future checks of information regarding age and life history from scale patterns, and are attached as electronic Appendices D (River Frome) and E (North Sea). Photograph codes are given in electronic Appendices B and C. The photographs also allow for illustration of scales where the portion to be dissected out and analysed was not immediately obvious, for reasons such as unclear winters or ill-defined summer growth periods, as shown in Figs. 2.4 and 2.5.

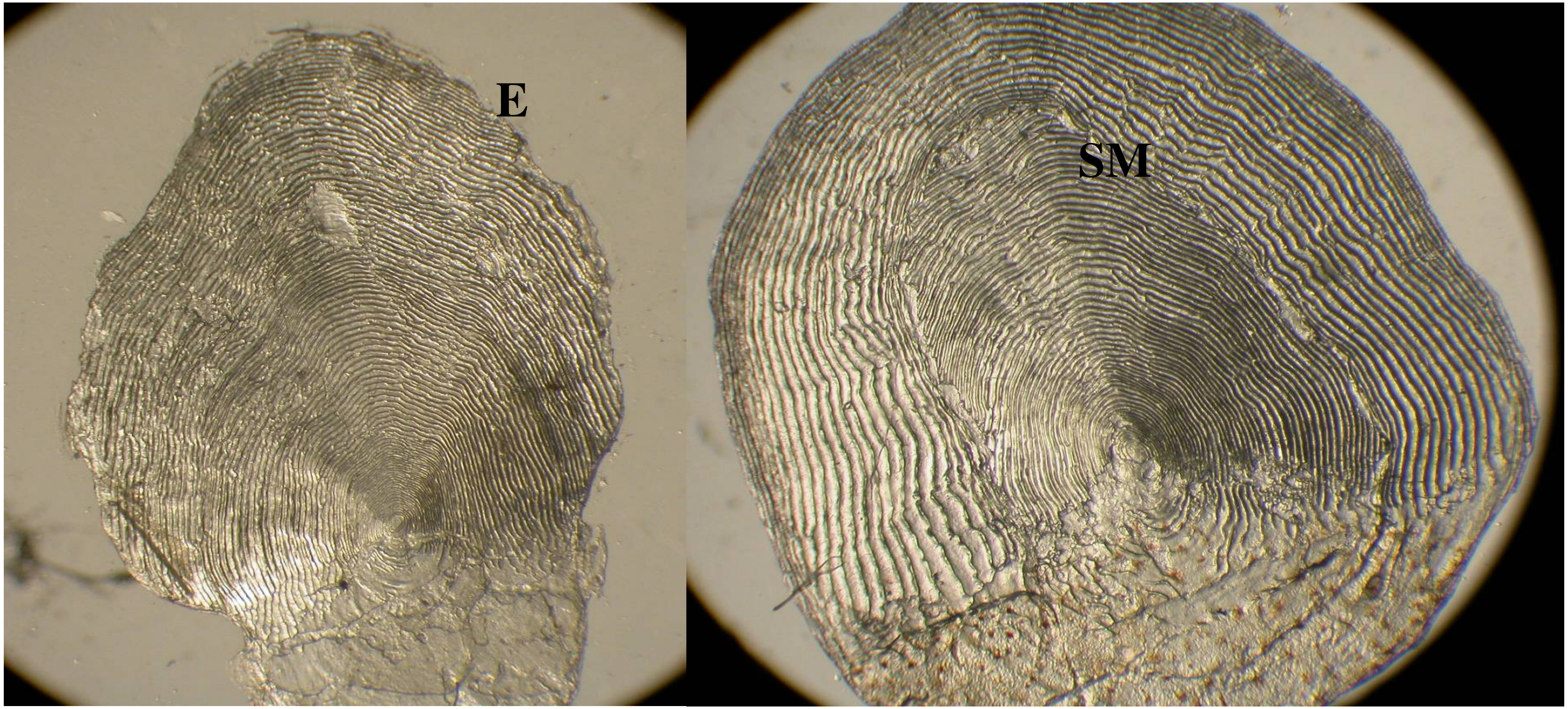
Before dissection, scales were briefly (c. 1-5 minutes) soaked in clean water, then blotted to remove excess water and cleaned on both sides using the reverse tip of a scalpel blade between the circuli, and the flat of the blade over the flat surfaces on both sides. This was done to remove adherents such as guanine and lipids. It was not deemed necessary to follow the decalcification technique of Perga & Gerdeaux (2003a) and Gerdeaux & Perga (2006), where scales were acid-washed in 1.2 mol L^{-1} HCL for 2 minutes prior to dissection and analysis in order to remove the bio-apatite layer. This decalcification technique is used to avoid any contamination from carbon in the bio-apatite, which is typically approximately 5‰ lighter in $\delta^{13}C$ than the collagen layer (Lee-Thorp et al. 1989). Elliott (2002) showed that carbon concentrations in bio-apatite are typically c. 1% by mass. In contrast, carbon concentrations in collagen are typically around 40% by mass. Hutchinson & Trueman (2006), demonstrated that bio-apatite:collagen ratios do not exceed 1:1 except in the few μm of the scale at the mineralisation front. Thus, the depleted bio-apatite $\delta^{13}C$ makes up less than 2.5% by mass of the total $\delta^{13}C$ for the scale sections analysed. In terms of the analytical values for natural abundance scale $\delta^{13}C$, the bulk $\delta^{13}C$ contribution from the bio-apatite layer is, therefore, below typical analytical precision of 0.2-0.3‰ (Hutchinson & Trueman 2006). This concurs with the work of Sinnatamby et al. (2007), who found that removal of the bioapatite layer from Atlantic salmon scales did not significantly affect stable isotope values when compared to non-acidified scales.

Dissection was carried out using a curved blade scalpel to cut out portions of the scale, and pointed forceps to hold the scale material down on a glass slide. Slides, scalpel and forceps were cleaned between each fish sampled. Sample portions were placed in paper envelopes labelled with archive name, date of capture, unique archive ID number and number of sample portions prior to preparation for mass spectrometry.



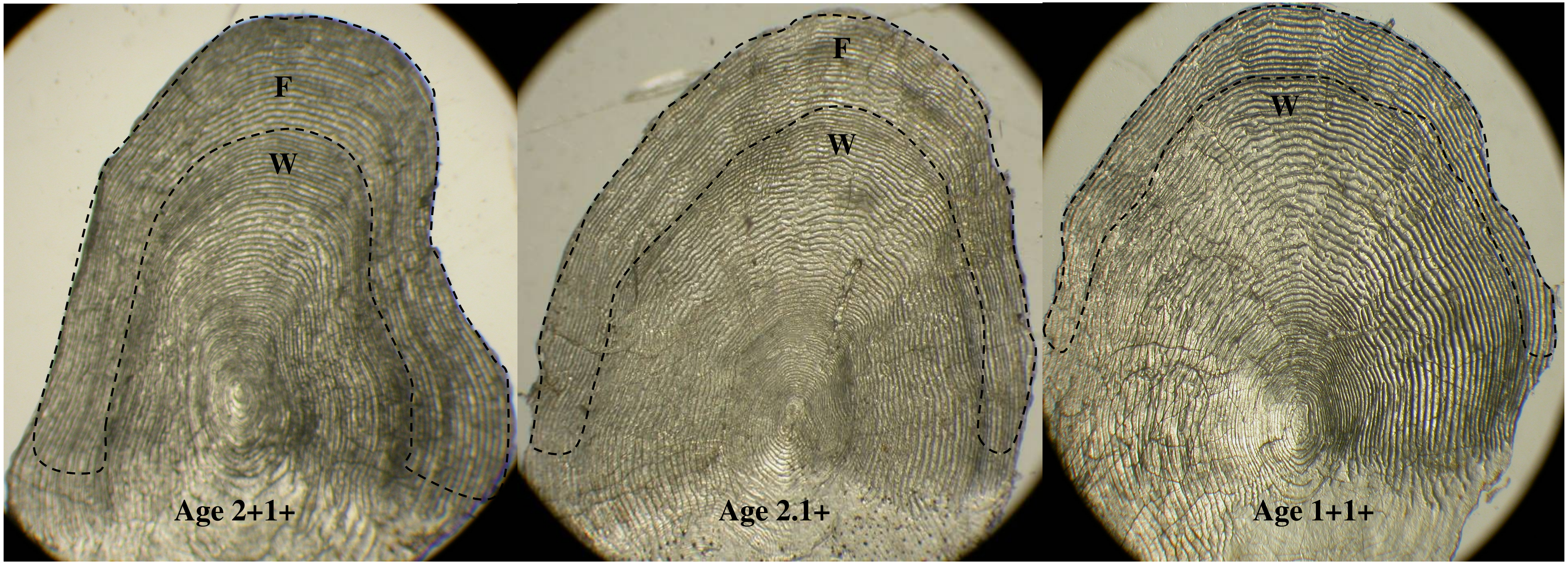
a) **b)**

Figure 2.2. Photomicrographs of scales from adult Atlantic salmon recovered from a) a grilse and b) a MSW fish returning to the natal river, indicating section removed for isotopic analysis (summer) and winter bands. W1: portion of scale laid down during 1st sea-winter, W2: portion of scale laid down during 2nd sea-winter; LS, portion of scale laid down during the last full season of growth at sea, to be removed for analysis.



a) **b)**

Figure 2.3. Photomicrographs of kelt (previous spawner) scales from adult Atlantic salmon recovered from a) a recent spawner b) a kelt that spawned the previous year. E: eroded edge of scale due to resorption from nutritional stress, SM: spawning mark – this marks previous erosion from spawning.



a) b) c)

Figure 2.4. Photomicrographs of grilse scales with difficult or ambiguous readings and dissection issues. The dashed line indicates portion of scale laid down during the last season of growth at sea, to be removed for isotopic analysis. W: portion of scale laid down during only sea-winter, F: false check, not to be confused with winter band. Note that the size of plus growth varies significantly, e.g. between scales a) and c), as does the clarity of the winter and the thickness of any check marks. a) shows a false check, which might be mistaken for a winter band that continues towards the edge of the scale; b) shows a false check, which again may be confused with a winter band, and also a very narrow sea winter band; c) shows a very small amount of plus growth to be sampled after the sea winter, and a poorly-differentiated sea winter band.

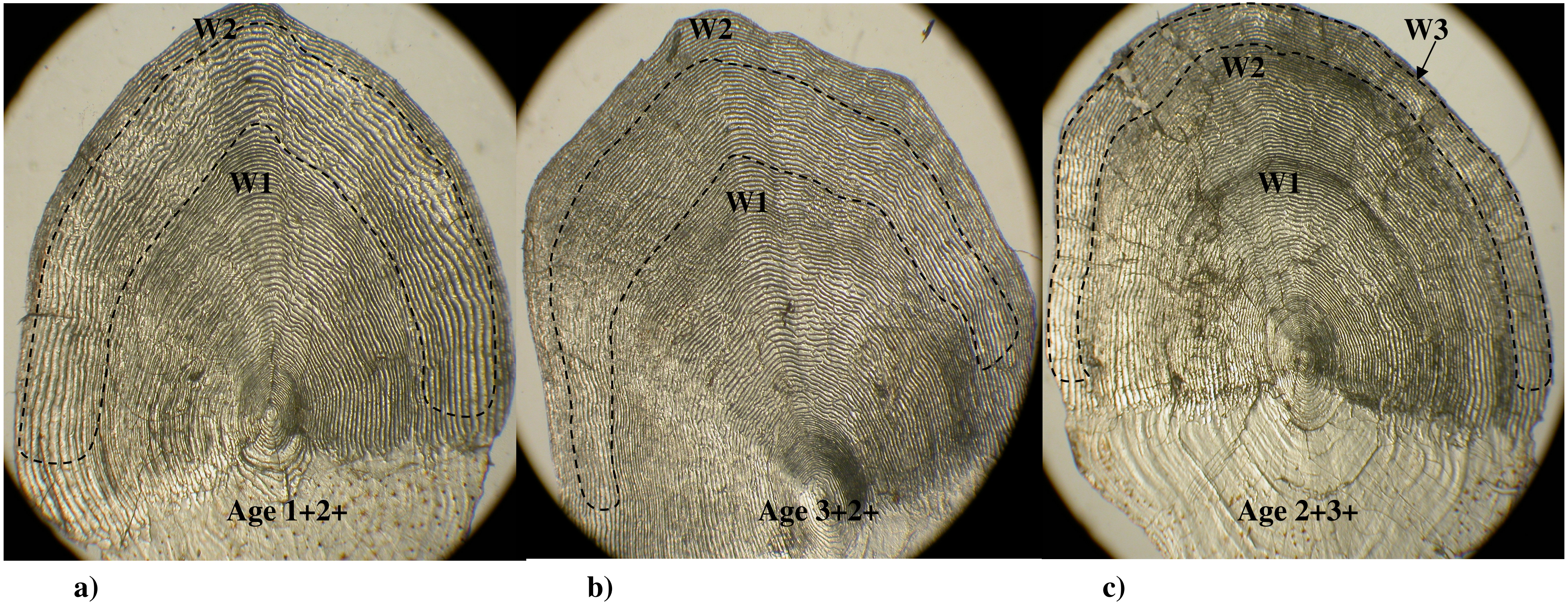


Figure 2.5. Photomicrographs of MSW scales with difficult or ambiguous readings and dissection issues. The dashed line indicates portion of scale laid down during the last full season of growth at sea, to be removed for isotopic analysis. W1-W3: portions of scale laid down during $1^{\text{st to 3rd}}$ sea-winters. Note the variable thickness of winter bands, with virtually nil winter and plus growth in scale c). a) shows minimal plus growth after W2, which might cause this fish to be identified as a grilse if note is not taken of the return date; b) shows densely-packed circuli throughout the marine section, with poorly-differentiated winter bands; c) shows a very thin portion of growth for the final season at sea, and a barely visible W3 band with no plus growth, again note must be taken of the return date to correctly age and dissect this scale.

Mass spectrometry protocol

Carbon and nitrogen isotope ratios for scale portions were measured by continuous-flow elemental analysis isotope ratio mass spectrometry (CF-EA-IRMS) using a EuroVector (model EA 3000) elemental analyser (EA) combined with a GV Instruments Isoprime mass spectrometer. Results were analysed using IonVantage software.

Approximately 0.5mg of each sample was combusted in a tin cup for the simultaneous determination of C and N isotope ratios. Three laboratory standards were analysed for every 12-16 samples in each analytical sequence, allowing instrument drift to be corrected if required, after the technique of Trueman *et al.* (2005). The measurement precision of $\delta^{15}N$ and $\delta^{13}C$ are, respectively, 0.7‰ and 0.1‰ (±2SD, based on 234 repeated analyses of laboratory standard ACROS L-glutamic acid).

Calibration to standard

Much time was spent calibrating the standards for comparative use to determine accuracy of the results produced by the EA-IRMS. Initially both ACROS L-alanine and ACROS L-glutamic acid were used, seeking the most consistent standard for use with the analyses. ACROS L-alanine, however, proved to be isotopically non-uniform throughout and was thus unreliable for use as a standard. The relative elemental per cent and isotopic per mil values for carbon and nitrogen in each potential standard, compared with approximate values for scale collagen are shown in Table 2.2.

Table 2.2. Relative compositions of scale collagen, ACROS L-glutamic acid, and ACROS L-alanine.

Material	C %	N %	$\delta^{13}C$‰ (wrt vPDB)	$\delta^{15}N$‰ (wrt Air)
Scale collagen	37	10	c. -13 to-20	c. 8 to 16
ACROS L-glutamic acid	41	10	-13.3	-3.9
ACROS L-alanine	41	16	-21.8	0.9

ACROS L-glutamic acid was chosen as the in-house standard as it yielded the most precise measurements (ACROS L-alanine ±2SD = 0.6 $\delta^{13}C$, n=24 and 0.1 $\delta^{15}N$, n=33), is the closest to scale collagen in per cent composition of C and N, which enables ease of use against the samples on the EA-IRMS. The in-house glutamic acid standard was calibrated against the USGS international standard L-glutamic acid, USGS40.

Refinement of isotope measurement techniques

Once a reliable standard had been chosen, tested and calibrated to international USGS standard, the technique was then refined in terms of EA-IRMS settings and scale sample mass for combined analysis on $\delta^{13}C$ and $\delta^{15}N$ for each sample. It was determined that an ideal scale mass should be between 0.5 and 0.6mg to produce a peak between approximately 5.0 and 6.6 nA, at no dilution on the nitrogen peak and c. 21 x dilution on the carbon peak. Scale samples of this mass were weighed, placed in tin capsules and crushed into cubes, attempting to ensure no air presence within the crushed capsule.

For each autosampler carousel (n = 39) on the EA-IRMS, a minimum of six ACROS L-glutamic acid standards was first run to test precision and stability of measurement. Samples were not run until standards showed stability and precision in measurement and blanks (empty, crushed tin capsules) showed effectiveness of burn. Nine further standards were included within each carousel of samples, divided into groups of 3 at the start, middle and end, to determine measurement drift for the duration of each sample carousel.

Quantifying intra-fish and population variation

In order to test the precision and accuracy of our protocols, experiments were run to determine variation in $\delta^{13}C$ and $\delta^{15}N$ in scale collagen within and between individual fish from a population of farmed salmon (fish scales supplied by EWOS), see Fig. 2.6, kept in the same tank and fed with the same feed.

Farmed fish isotope values were tested for normality using the Anderson-Darling test. The $\delta^{13}C$ values were normally distributed (p=0.427, n=29), but the $\delta^{15}N$ values were not (p=0.005, n=29). The variation (±2 SD) within individual farmed fish ($\delta^{13}C$ =0.3, $\delta^{15}N$ = 0.7, n=6.88) was found, using Levene's test, to be significantly greater than the variation of the analytical standard ACROS L-glutamic acid for both nitrogen (p = 0.04, W = 2.02, df = 233) and carbon (p = 0.002, W = 3.19, df = 233). A power analysis was used to estimate of the number of scale samples required to provide a representation of individual salmon mean $\delta^{13}C$ and $\delta^{15}N$ accurate to +/- 10% with 95% confidence, according to the following equation:

$$n \approx \frac{t^2 s^2}{(p\bar{y})^2}$$

(after Eckblad 1991). Where n is the number of samples, t is the value of the t-distribution corresponding to the sample number (degrees of freedom) and confidence level (0.05), s is the standard deviation, p is the precision required, and $\bar{y}$ is an estimate of the mean. Given the measured variation within seven scale samples of the most variable individual salmon ($\delta^{15}N$ s = 0.35, $\bar{y}$ = 10.7; $\delta^{13}C$ s = 0.16, $\bar{y}$ = -17.4), less than a single scale sample was required to constrain $\delta^{15}N$ and $\delta^{13}C$ values at a precision of 0.1 or $\delta^{13}C$ values at a precision of 0.05, and approximately 2.5 scale samples for $\delta^{15}N$ values at a precision of 0.05.This indicates that a single scale provides a reasonably reliable measurement of the isotopic composition of collagen within an individual fish, although between one and five scale samples were subsequently included in each fish measured for reasons of sample mass. Using Levene's test, $\delta^{15}N$ and $\delta^{13}C$ variation between scales within a single fish was also found to be significantly less than variation between fish from the same population ($\delta^{15}N$ W = 17.56, p = 0.025; $\delta^{13}C$ W = 2.33, p = 0.025).

To assess the variation between fish from a single wild cohort, scales were analysed from 23 fish captured from a wild population in 2002 in Poole Bay (samples provided by the Wessex Salmon and Rivers Trust, WSRT), near the outflow of the River Frome. Poole Bay fish isotope values were then tested for normality using the Anderson-Darling test. It was found that $\delta^{15}N$ values were normally distributed (p=0.491, n=23), but the $\delta^{13}C$ values were not (p=0.018, n=23). Between-fish variance in the Poole Bay population ($\delta^{13}C$ 2SD = 0.12, $\delta^{15}N$ 2SD = 0.48, n = 23) was found, again using Levene's test, to be significantly greater in $\delta^{13}C$ than variation between the farmed fish (W = 13.1, p = 0.001), and in $\delta^{15}N$ (W = 36.81, p < 0.001). See Fig. 2.6 for graphical representation of data tested above.

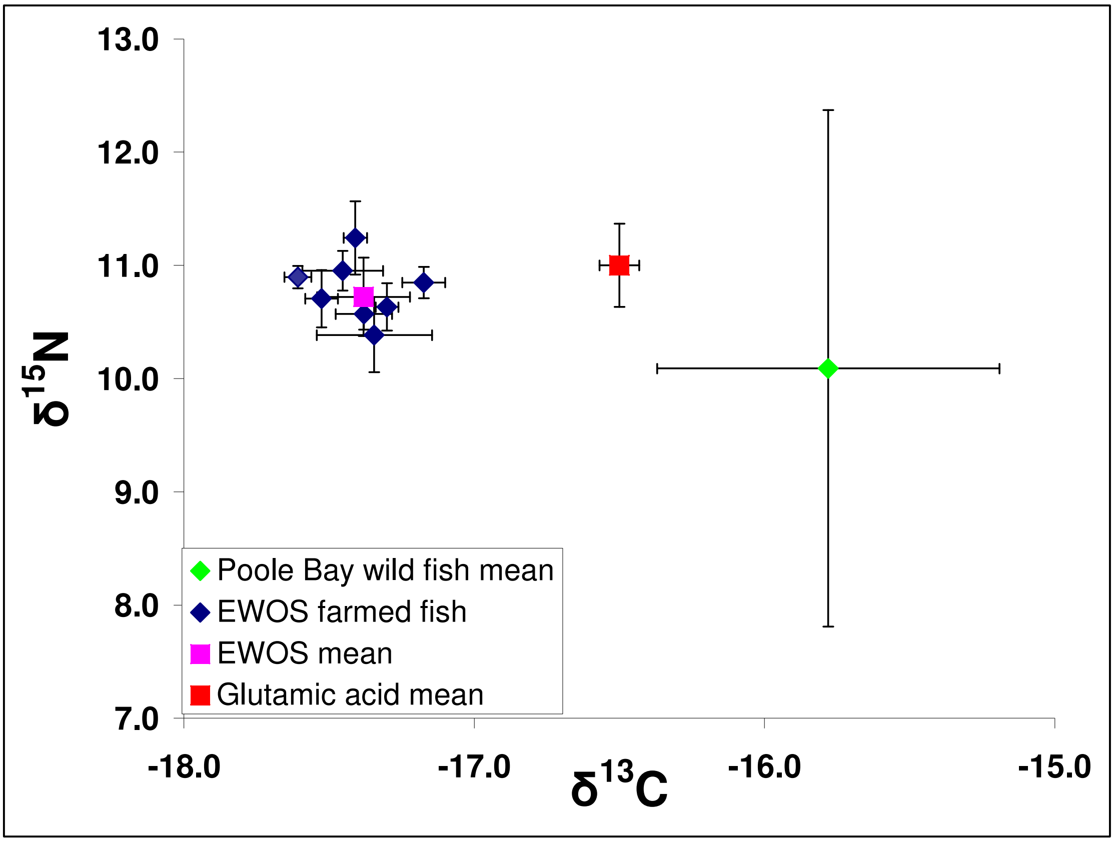


Figure 2.6. Variation within and between individuals from a population of farmed fish, compared with analytical standard variation and variation within a population of wild fish from Poole Bay. Symbols are ±1 SD.

The power analysis equation used to quantify intra-fish variation above was used here to estimate of the number of samples required to provide a representation of population mean $\delta^{13}C$ and $\delta^{15}N$ accurate to +/- 5% with 95% confidence (after Eckblad 1991).

Given the measured variation between 23 fish within the wild Poole Bay population ($\delta^{15}N$ s=2.28, $\bar{y}$=10.09; $\delta^{13}C$ s=0.59, $\bar{y}$=-15.78), approximately 20 fish were required to constrain $\delta^{15}N$ values at a precision of 0.1, and approximately 2 fish for $\delta^{13}C$ values at a precision of 0.05. For the sake of accuracy and precision, and for practical considerations of time, cost and sample availability, it was decided to sample approximately 10 grilse and 10 MSW fish, dependent on availability, per archive per year; this number allowed constraint of approximately 85% of variation in $\delta^{15}N$ values.

Test of the ability of the sampling strategy to recover trophic information

Using the methodology detailed above, a test was devised to determine whether a difference between two nutritionally dissimilar groups of salmon could be measured. Cefas provided scales from a number of wild-caught salmon on return to unnamed rivers. These scales were from two groups of fish: some unusually thin for their length and some normal. The scales from these fish were blind-tested to determine whether the isotope ratios of $\delta^{15}N$ to $\delta^{13}C$ could be used to identify the thin salmon from the normal salmon. The N:C isotope ratio might be expected to be relatively higher in thinner fish due to greater self-catabolism during return spawning migration than more normal fish; the mechanisms responsible for this are discussed in more detail in section 2.2 (Stable Isotope Analysis (SIA) and background) in the Introduction chapter. The results of these analyses are shown below in Fig. 2.7., with the post-analysis differentiation between thin and normal fish revealed.

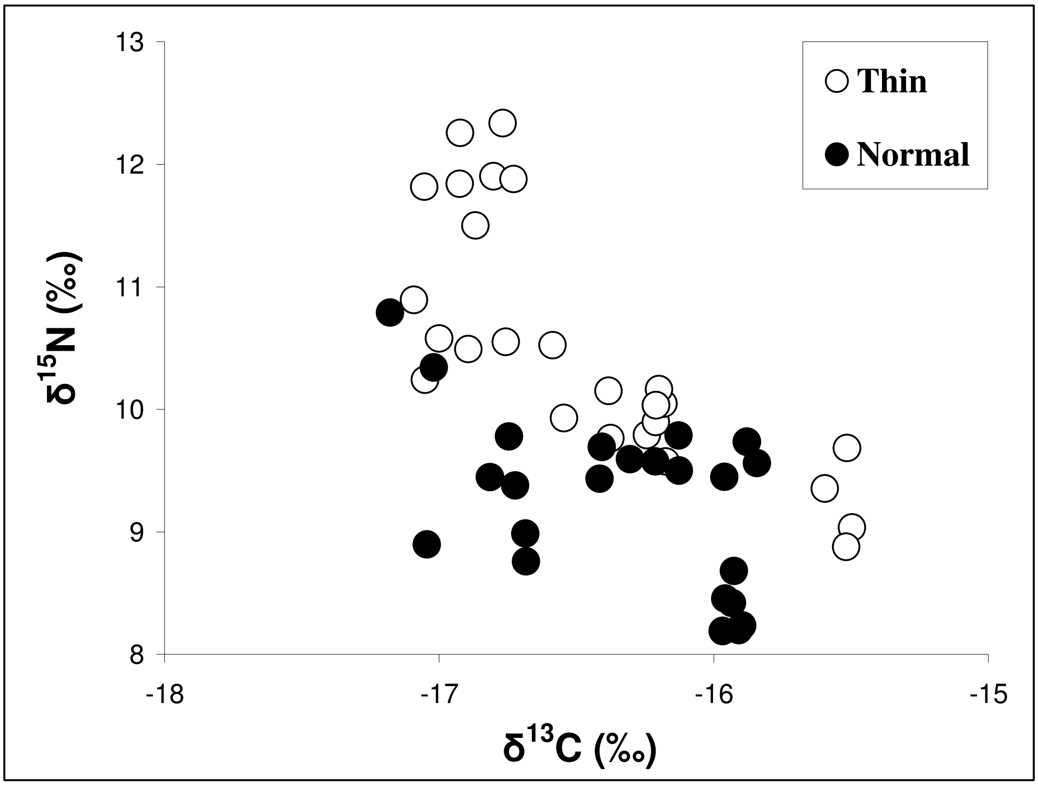


Figure 2.7. N:C ratios for blind-tested thin and normal salmon scale samples provided by Cefas. Thin salmon results are empty circles, normal salmon results are filled circles.

As shown in Fig. 2.7, thin fish were significantly enriched in ^{15}N compared to normal fish (thin: fat n = 26: 24, $p < 0.001$) but no significant difference was found in

$\delta^{13}C$ values (thin, fat n = 26,24, p = 0.15). These datasets were non-normal, thus Mann-Whitney U tests were used to determine differences. Based on these analyses, it may be concluded that information on the nutritional status of salmon may be gained from the ratio of $\delta^{15}N$ to $\delta^{13}C$. If there are fish in normal, i.e. non-starved, condition with which to compare samples according to the methods detailed above, it would be expected that fish with higher levels of self-catabolism should show relatively elevated $\delta^{15}N$ to $\delta^{13}C$ ratios.

3. Results and discussion – Trophic levels and migration

All carbon and nitrogen isotope values from analyses carried out on archived scale samples taken from grilse and MSW salmon caught in the River Frome (RF) and Northeast Coast (NEC) are shown below in Figs 3.1 & 3.2, and presented in electronic Appendices B & C as part of the River Frome and Northeast Coast archive databases.

Overall, grilse from the River Frome stock analysed (n = 183) had a mean δ^{13}C value of -16.0 ‰ (±0.54 SD, min = -18.4, max = -15.0), and a mean δ^{15}N value of 9.8 ‰ (±1.07 SD, min = 5.9, max = 12.6); MSW fish from this stock (n = 141) had a mean δ^{13}C value of -16.5 ‰ (±0.48 SD, min = -18.1, max = -15.3), and a mean δ^{15}N value of 11.2 ‰ (±0.73 SD, min = 8.9, max = 12.9) data. Grilse from the Northeast Coast salmon analysed (n = 150) had a mean δ^{13}C value of -15.6‰ (±0.79 SD, min = -17.6, max = -13.4), and a mean δ^{15}N value of 10.0‰ (±1.50 SD, min = 7.0, max = 14.8); MSW fish from this stock (n = 139) had a mean δ^{13}C value of -15.5‰ (±0.83 SD, min = -18.1, max = -13.5), and a mean δ^{15}N value of 10.5‰ (±0.76 SD, min = 8.5, max = 12.6), see also Table 3.1 for summary data.

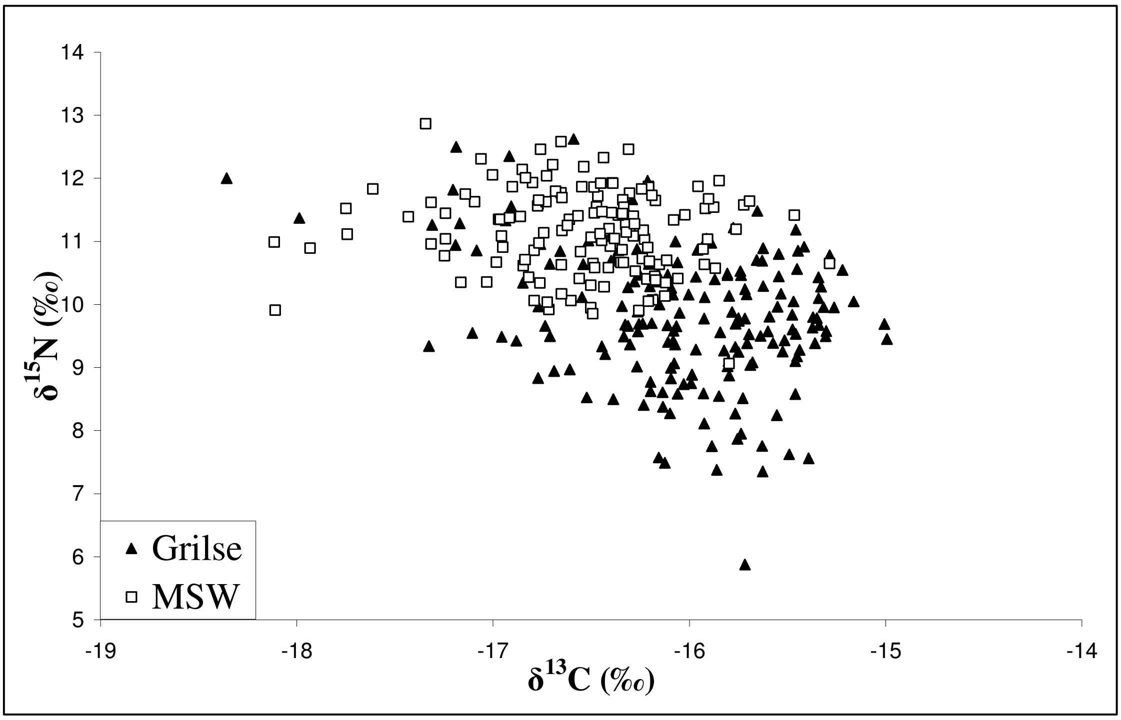


Figure 3.1. Scatter plot of all results from analyses to date of River Frome archive scales for δ^{13}C and δ^{15}N values; filled triangles denote grilse, empty squares denote MSW fish.

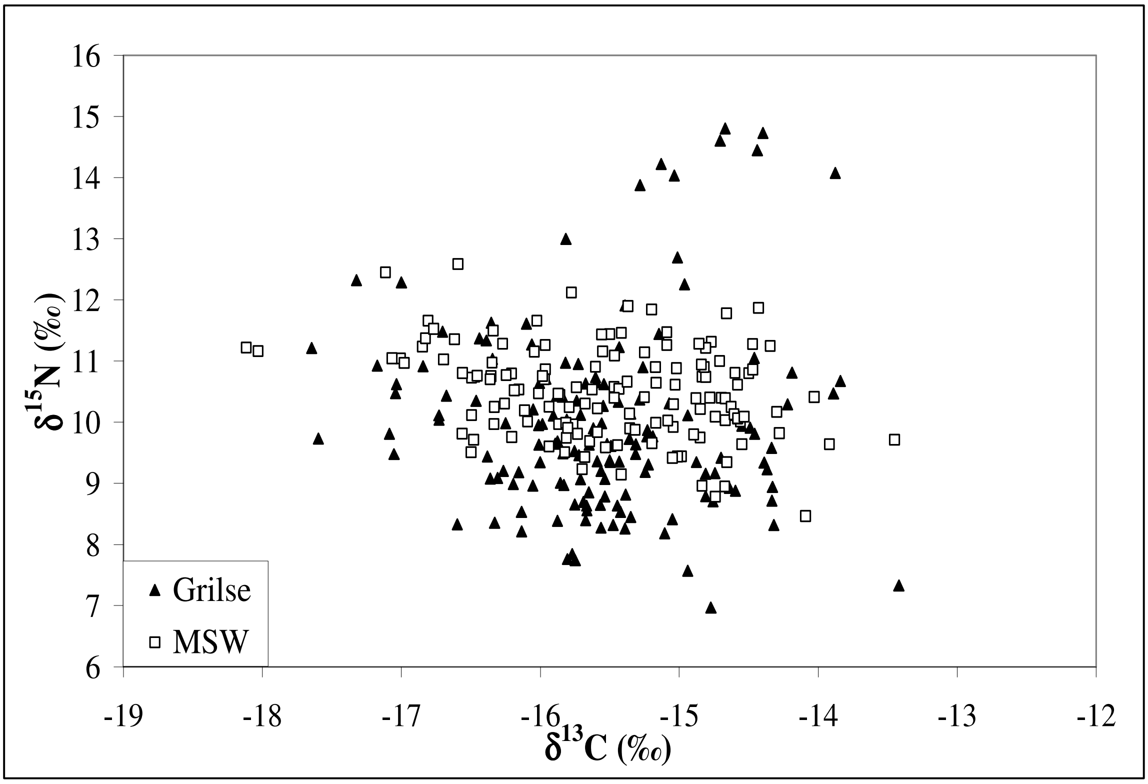


Figure 3.2. Scatter plot of all results from analyses of Northeast Coast driftnet archive scales for $\delta^{13}C$ and $\delta^{15}N$ values; filled triangles denote grilse, empty squares denote MSW fish.

If variation in both C and N isotopes were controlled purely by trophic fractionation, a positive linear correlation between $\delta^{15}N$ and $\delta^{13}C$ would be expected, with a slope of c.2 (Trueman et al. 2005). The absence of such a correlation, see Figs 3.1 & 3.2, indicates that there are additional mechanisms controlling $\delta^{15}N$ and $\delta^{13}C$ values in River Frome and Northeast Coast salmon scales, for both grilse and MSW fish. Grilse show greater variation in $\delta^{15}N$ values than MSW salmon in both populations (F tests RF grilse, RF MSW: n = 183, 141, F = 2.15, $p < 0.001$; NEC grilse, NEC MSW: n = 150, 139, F = 3.96, $p < 0.001$), but the variation in $\delta^{13}C$ values is not significantly different between cohorts from either population (RF grilse, RF MSW: F = 1.27, p = 0.14; NEC grilse, NEC MSW: F = 0.91, p = 0.56).

Table 3.1. Summary of results from all analyses for $\delta^{13}C$ and $\delta^{15}N$ values (‰) on River Frome (RF) and Northeast Coast (NEC) salmon scales.

Cohort	**n**	**Mean $\delta^{13}C$ value ‰ (±SD)**	**Mean $\delta^{15}N$ value ‰ (±SD)**
RF Grilse	183	-16.0 ±0.54	9.8 ±1.07
RF MSW	141	-16.5 ±0.48	11.2 ±0.73
NEC Grilse	150	-15.6 ±0.79	10.0 ±1.50
NEC MSW	139	-15.5 ±0.83	10.5 ±0.76

3.1. Overall isotopic differences between grilse and MSW fish

Based on the larger size of MSW fish (Nowak et al. 2004), it was hypothesised that grilse feed at a lower trophic level than MSW, and that this would be demonstrated by higher $\delta^{15}N$ values in MSW fish. It was also hypothesised that there would be no observable separation in feeding location between grilse and MSW fish, demonstrated by $\delta^{13}C$ values propagated up the foodweb from the same source primary production. These hypotheses were tested by ANOVA in Minitab® statistical software, the results of which are shown in Table 3.2.

Table 3.2. Results of ANOVAs on $\delta^{13}C$ and $\delta^{15}N$ values between cohorts from the River Frome and Northeast Coast. Bold p values denote significance at $\alpha = 0.05$.

ANOVA	**n**	**df**	**F**	**p**
$\delta^{13}C$ River Frome Grilse vs MSW	183, 141	1	76.75	**<0.001**
$\delta^{15}N$ River Frome Grilse vs MSW	183, 141	1	165.34	**<0.001**
$\delta^{13}C$ Northeast Coast Grilse vs MSW	150, 139	1	0.26	0.61
$\delta^{15}N$ Northeast Coast Grilse vs MSW	150, 139	1	12.72	**<0.001**

Table 3.3. Results of ANOVAs on $\delta^{13}C$ and $\delta^{15}N$ values between the River Frome and Northeast Coast cohorts. Bold p values denote significance at $\alpha = 0.05$.

ANOVA	**n**	**df**	**F**	**p**
$\delta^{13}C$ RF Grilse vs NEC grilse	183, 150	1	41.09	**<0.001**
$\delta^{15}N$ RF Grilse vs NEC grilse	183, 150	1	1.60	0.21
$\delta^{13}C$ RF Grilse vs NEC MSW	183, 139	1	45.74	**<0.001**
$\delta^{15}N$ RF Grilse vs NEC MSW	183, 139	1	40.97	**<0.001**
$\delta^{13}C$ RF MSW vs NEC MSW	141, 139	1	161.55	**<0.001**
$\delta^{15}N$ RF MSW vs NEC MSW	141, 139	1	57.05	**<0.001**
$\delta^{13}C$ RF MSW vs NEC grilse	141, 150	1	160.74	**<0.001**
$\delta^{15}N$ RF MSW vs NEC grilse	141, 150	1	70.67	**<0.001**

3.2. Explanation of differences in δ^{15}N values

Baseline δ^{15}N variation is highly variable in the open ocean (Jennings et al. 2008a; Jennings & Warr 2003; Lara et al. 2010; McClelland & Montoya 2002; Tamelander et al. 2009; Waser et al. 2000), which means that it is not currently possible to determine prey sources with any meaningful level of precision. It is possible with such a large dataset, however, to make strong comparative inferences of trophic position between cohorts within and between populations (Graham et al. 2010).

As predicted, the mean nitrogen isotope compositions of scales are significantly different between grilse and MSW fish in both populations, see Table 3.2, with higher δ^{15}N values in MSW salmon, indicating that the larger MSW fish are feeding at a higher trophic level to grilse (assuming a common baseline δ^{15}N level). The separation between grilse and MSW fish indicates that, given an approximate δ^{15}N tissue-diet spacing of 2.1 ‰ in the scale tissue of Atlantic salmon (Trueman et al. 2005), there is a separation of *c.* two thirds of a trophic level between the River Frome cohorts, and *c.* a quarter of a trophic level between the Northeast Coast cohorts. The mean value of the River Frome grilse δ^{15}N data does not change if the outlier at 5.9‰ is removed (data point from a 1 nA measurement signal, confirmed as an outlier by box & whisker analysis = 1.15 * the interquartile, IQ, range below the lowermost limit of the whisker, = 2.61 * IQ below the lower limit of the box). In the Northeast Coast salmon, however, the mean value of the grilse δ^{15}N data decreases to 9.7‰ (± 1.11 SD) if the outliers over 13‰ are removed (data points all from a single mass spectrometry run, confirmed as outliers by box & whisker analysis = 0.79 to 1.41 * the interquartile, IQ, range above the uppermost limit of the whisker, = 2.70 to 3.39 * IQ above the upper limit of the box). This removal increases the difference between the cohorts (δ^{15}N grilse: MSW fish, $n = 142, 139$, $F = 43.68$, $p < 0.001$). Without these outliers, there is a separation of *circa* 0.3 of a trophic level between the cohorts of salmon from the Northeast Coast. The δ^{15}N values noted as outliers are excluded from any further analyses on the River Frome and Northeast Coast.

The observed between cohort separation in δ^{15}N values for both populations is likely due to the difference in mass between the two cohorts, with the larger MSW fish able to consume larger prey items higher up in the marine trophic web than the grilse, due to concurrent increase in gape size and ability to capture larger prey (Christensen 1996; Scharf et al. 2000). The fact that there is not a full trophic level separation between the cohorts of either population may be indicative of size variation within each cohort, creating trophic overlap, and of variation in baseline ecosystem $\delta^{15}N$ values, which also control tissue $\delta^{15}N$ values (Graham et al. 2010). It is surprising that the difference in $\delta^{15}N$ values is smaller between the Northeast Coast cohorts than that seen between River Frome grilse and MSW salmon as the mean masses for each cohort are similar between the two populations (see section 3.4, below), The SD values (minus the outliers) for each age class are similar, however, which suggests that baseline $\delta^{15}N$ variation may exert a stronger control on Northeast Coast salmon $\delta^{15}N$ values than trophic level. Baseline variation in marine $\delta^{15}N$ values is controlled by a variety of factors, including nitrate concentrations, temperature, primary productivity, rate of phytoplankton uptake, nitrogen source, phytoplankton taxonomic composition, salinity, depth, upwelling and proximity to land (Jennings & Warr 2003; Mendes et al. 2007; Switzer et al. 2003; Taylor et al. 1993; Van Hale & Frew 2010; Waser et al. 2000).

Based on stomach contents data, Jacobsen and Hansen (2001) showed that Atlantic salmon demonstrate preferential feeding, with fish preferred to crustaceans and amphipods preferred to euphausiids; larger salmon were also more piscivorous than smaller salmon. Fish appear to be the most desirable source of prey throughout the marine life of Atlantic salmon, with higher post-smolt condition factors correlating with greater incidence of fish larvae, particularly herring, in feeding grounds and stomachs of post-smolts (Haugland et al. 2006). Prey types appear dependent on availability and size of desirable prey items, indicating that size and capture ability are limiting factors throughout the life history of salmonid fish (Andreassen et al. 2001; Brodeur 1991; Hansen et al. 2003; Jacobsen & Hansen 2001). The published data describing higher incidence of fish in stomachs of larger salmon are consistent with the observed increase in $\delta^{15}N$ values in larger MSW salmon, which are more able to capture and consume larger, more energetically desirable, higher trophic level, faster and more manoeuvrable fish. Smaller grilse have correspondingly smaller gapes and less power to accelerate, so consume relatively lower trophic level, slower invertebrates (Christensen 1996; Lundvall et al. 1999; Scharf et al. 2000). This higher trophic level feeding for MSW fish is supported by a greater range of $\delta^{15}N$ values in grilse, confirmed by the F test results in section 3 above. This indicates a wider trophic niche, more variable baseline $\delta^{15}N$ values, or both in grilse than MSW salmon.

3.3. $\delta^{13}C$ values

The mean carbon isotope compositions of scales from the River Frome grilse and MSW fish are significantly different, see Table 3.2, with MSW salmon having lower $\delta^{13}C$ values. The mean value of $\delta^{13}C$ for River Frome MSW salmon is -16.5‰ (±0.48 SD), and -16.0‰ (±0.54 SD) for River Frome grilse. In contrast, there is no significant difference between the $\delta^{13}C$ values of grilse and MSW fish from the Northeast Coast, see Table 3.2. The mean value of $\delta^{13}C$ for Northeast Coast MSW salmon is -15.5‰ (±0.83 SD), and -15.6‰ (±0.79 SD) for Northeast Coast grilse. If there were a trophic control on $\delta^{13}C$ values, these would be expected to increase with mass and MSW fish would be expected to have higher $\delta^{13}C$ values than grilse. As shown in Figs 3.1 & 3.2, the opposite is true in River Frome salmon, and there is no significant difference in the $\delta^{13}C$ values of Northeast Coast grilse and MSW fish. The isotopic composition of carbon in tissues of pelagic marine fish is strongly dependent on that of phytoplankton at the base of the marine food chain (Barnes et al. 2009; Vander Zanden & Rasmussen 1999), which is in turn dependent on plankton growth rates, the concentration of aqueous CO_2 in seawater, salinity, and light intensity. All of these variables are either directly or indirectly related to sea surface temperature (Hofmann et al. 2000; Popp et al. 1989; Rau et al. 1996; Switzer et al. 2003; Tamelander et al. 2009). There is also a small effect on baseline $\delta^{13}C$ signatures from primary production taxonomy, particularly in a prevalence of diatoms as these tend to be enriched in ^{13}C relative to the rest of the primary productivity, in part due to relatively higher growth rates (Kukert & Riebesell 1998; Lara et al. 2010; Popp et al. 1998). Strong blooms of specific taxa are, by their nature, short lived (Bax et al. 2001; Taylor et al. 1993); this means that their isotopic signature would form a small part of the overall integrated value of the assimilation period for slow growing tissues with little or no turnover. Given that these scale analyses represent the integrated isotopic values from approximately eight months of growth over a summer season, small spatial, temporal and taxonomic differences in the carbon isotope composition of the food web during this period are likely to be insignificant when compared to the SST-related basal ecosystem signature. Hence, differences in $\delta^{13}C$ values between cohorts and populations of salmon indicate differences in conditions experienced at sea over the full summer of growth, and therefore differences in location. These data provide the first evidence for stock separation between cohorts from the same river of origin and between populations of salmon from relatively close natal origins in the marine environment. Where fish perform consistent migrations over time, temporal patterns of variation in tissue $\delta^{13}C$ values will co-vary with those of local SST.

Different feeding locations at sea may have implications for analyses of both $\delta^{13}C$ and $\delta^{15}N$ values of salmon scales, as it is likely that differences in baseline $\delta^{13}C$ values will exist alongside differences in baseline $\delta^{15}N$ values.

3.4. $\delta^{13}C$ and $\delta^{15}N$ values and relationships with mass

Data were investigated by regression to test whether the isotopic ratio values displayed any relationship with body mass (in kg). In a size-structured ecosystem with a constant baseline $\delta^{15}N$ value, $\delta^{15}N$ values would be expected to covary positively with mass (Jennings et al. 2008a; Jennings et al. 2008b), as explained more fully in the Introduction chapter. Indeed, unless ecosystem baseline $\delta^{15}N$ variation is very large, there should generally be a positive relationship between mass and $\delta^{15}N$ values in salmon. In the River Frome salmon population MSW fish have significantly higher mass than grilse (non-normal mass data for both cohorts, Mann-Whitney U test, grilse, MSW: n = 180, 130, W = 17543, $p < 0.001$). Mass is also significantly higher for MSW fish than grilse in the Northeast Coast population (Mann-Whitney U test, grilse, MSW: n = 94, 75, W = 4574, $p < 0.001$). Interestingly, grilse and MSW fish in both populations had similar mean masses (mean mass (kg): RF grilse: 3.2, NEC grilse: 3.0, RF MSW: 6.0, NEC MSW: 6.3), indicating that there may be a mass component involved in the decision of how long to remain at sea before return migration.

Variable mass and, therefore, variable nitrogen isotope ratios due to differential trophic status between years, cohorts, stocks and populations would make interpretation of isotopic variation at the base of the ecosystem difficult without correction for any mass effects. If mass does covary with $\delta^{15}N$ values, then a mass correction should be applied in order to remove the mass-related isotopic variation in order to interpret the variation at the base of the ecosystem. Plots of River Frome $\delta^{15}N$ and $\delta^{13}C$ values against mass are shown in Fig. 3.3 (a&b) and Northeast Coast values in Fig. 3.4 (a&b). Mass values for both populations lie along a growth continuum, thus no distinction between cohorts was made in the regressions.

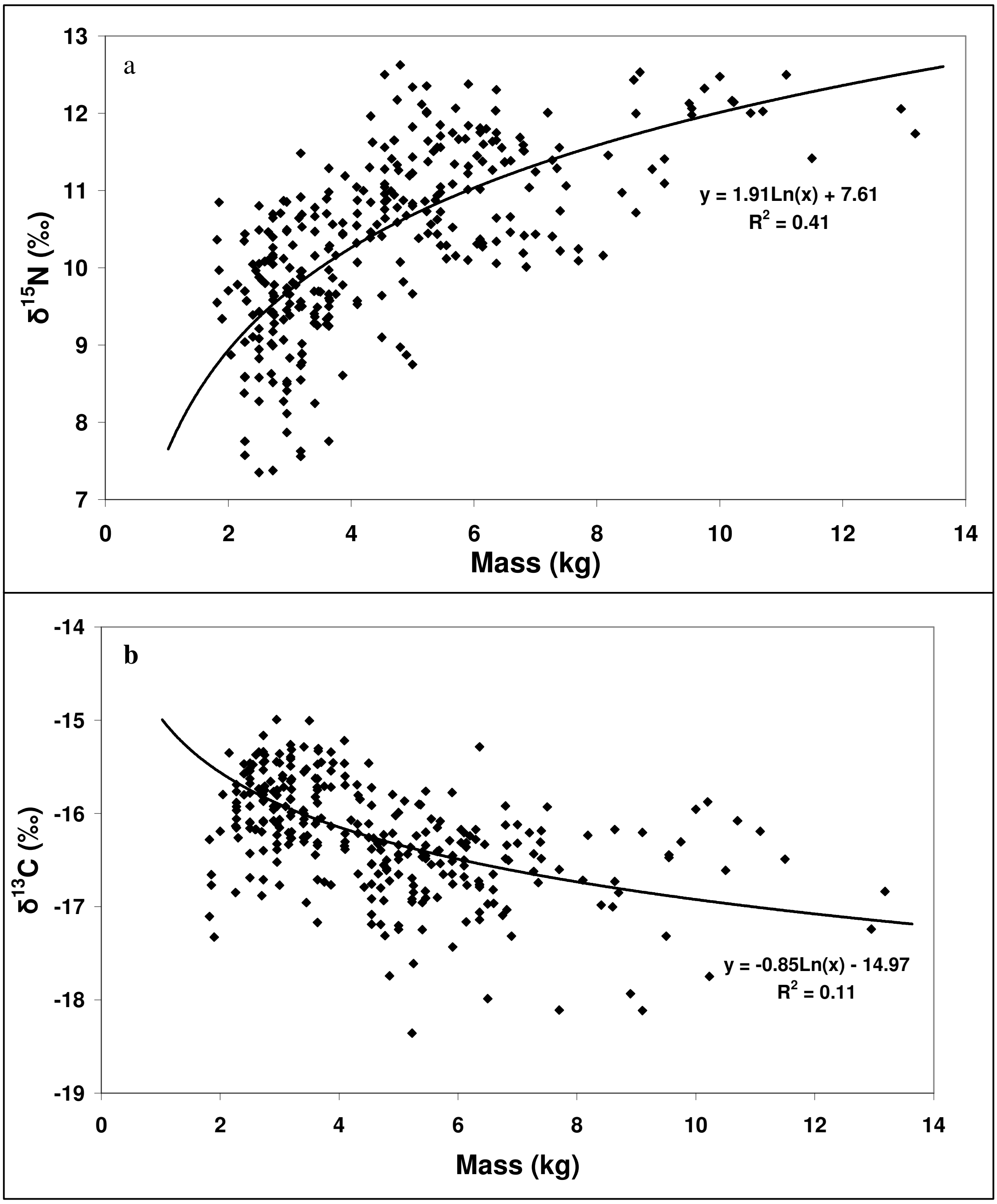


Figure 3.3. Scatter plots of data from River Frome salmon showing a) relationship between mass (kg) and $\delta^{15}N$ values (‰, outlier removed), and b) relationship between mass (kg) and $\delta^{13}C$ values (‰). Equation and R^2 value for each linear regression are shown; p-values are in the text below. Fish with no record of mass were excluded from the analyses (missing grilse: n = 3, missing MSW: n = 11).

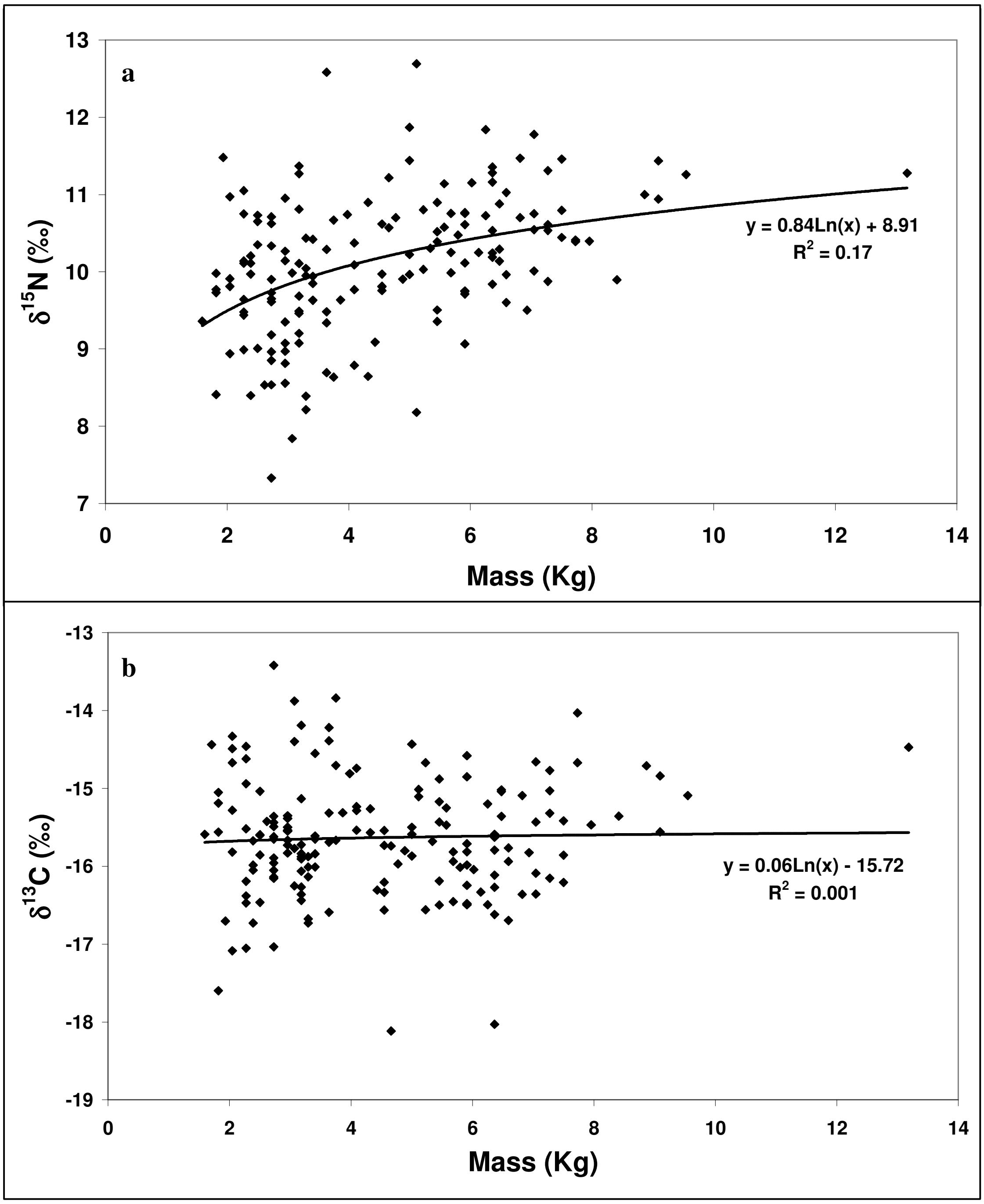


Figure 3.4. Scatter plots of data from Northeast Coast salmon showing a) relationship between mass (kg) and $\delta^{15}N$ values (‰, outliers removed), and b) relationship between mass (kg) and $\delta^{13}C$ values (‰). Equation and R^2 value for each linear regression are shown; p-values are in the text below. Fish with no record of mass were excluded from the analyses (missing grilse: n = 56, missing MSW: n = 64).

Nitrogen

Significant, positive relationships exist between body mass and δ^{15}N values for both River Frome and Northeast Coast fish (RF salmon: n = 309, R^2 = 0.41, $p<0.001$; NEC salmon: n = 169 R^2 = 0.17, $p<0.001$), see Figs 3.3a & 3.4a. These positive relationships between δ^{15}N values and mass for both grilse and MSW fish suggest that trophic level is a major factor in determining δ^{15}N values for these fish (DeNiro & Epstein 1981; Wada et al. 1991a; Wada et al. 1991b). A size-structured ecosystem is, by definition, one where mass and trophic level in predatory marine species are intrinsically linked (Barnes et al. 2010; Jennings et al. 2008a; Jennings et al. 2008b; Jennings et al. 2001b), therefore it might be concluded that the Atlantic salmon populations investigated here are strongly size-structured. The structuring is different between the populations, however, with a different size equation for River Frome and Northeast Coast fish. Deviation from the logarithmic relationships between δ^{15}N values and mass for these fish (Figs 3.3a & 3.4a) may indicate baseline variations in δ^{15}N values (Graham et al. 2010; Olson et al. 2010), differences in prey types consumed by the populations, or nutritional status of the fish (Best & Schell 1996; Vanderklift & Ponsard 2003; Waddington et al. 2008). An alternative, though less likely, interpretation is that the salmon grow larger under conditions of more positive baseline δ^{15}N values.

The slope of the relationship between δ^{15}N values and mass is higher in River Frome (1.91) than Northeast Coast fish (0.84), indicating the possible existence of greater ecosystem trophic structuring in the feeding grounds used by salmon from the River Frome than those of the Northeast Coast fish. The logarithmic nature of the δ^{15}N to mass relationships in both populations indicates that the smaller fish (predominantly grilse) may have more rapid and developmental growth, with a concurrent rapid increase in gape size, enabling them to feed on increasingly larger fish, thus their upper values of δ^{15}N are limited by their growth. In contrast, the larger (predominantly MSW) salmon are not growing as rapidly, nor does their gape size increase substantially with mass, thus they display lower trophic level increase with mass (Keeley & Grant 2001). The inflexion of the relationships between the smaller and larger salmon in both populations have a critical mass value of around 4-5kg where fish likely change from rapidly switching prey types and increasing in trophic levels to a more stable, preferentially piscivorous diet.

On comparing the cohorts from the two populations, it appears that, despite the ability to feed across many size classes, MSW fish maintain selectivity for larger prey, as their $\delta^{15}N$ value range is narrow, but their size range (RFM SD = 1.92; NECM SD = 1.47) is much larger than that of grilse (RFG SD = 0.98; NECG SD = 0.83) (F test (mass) RF grilse, RF MSW: n = 180, 130, F = 0.26, $p < 0.001$; NEC grilse, NEC MSW: n = 94, 75, F = 0.32, $p < 0.001$). These hypotheses are supported by the grilse having significantly greater variance in $\delta^{15}N$ values, potentially indicating more obligate opportunism in their feeding strategy, than MSW fish, as detailed in section 3.1. The MSW fish may also be able to feed more selectively due to slower growth rates and greater energy reserves in the larger fish (Keeley & Grant 2001). The similarities in patterns shown by the two populations of salmon suggest that there is a marked difference in dietary behaviour between fish under 4-5kg, which are generally grilse, and fish of greater mass, which are generally MSW salmon.

Other factors that may explain the logarithmic nature of the size equations include higher tissue turnover rates in the smaller, faster growing fish leading to greater fractionation and faster incorporation of isotopically fractionated products into tissues (Jennings et al. 2008b), different compositions of prey items, or flatter trophic structure in areas frequented by larger fish, or fish from the Northeast Coast population (Barnes et al. 2010; Cabana & Rasmussen 1996). It is useful to explore the $\delta^{15}N$ data both uncorrected and mass corrected in order to investigate trophic level effects and size-structuring within the salmon cohorts and populations, together with wider ecosystem effects. Baseline variation in $\delta^{15}N$ values will add to residual variation about the regression slopes, and any mass effect must be removed in order to investigate these baseline ecosystem $\delta^{15}N$ values without bias caused by differential size effects.

Carbon

A negative relationship exists between body mass and $\delta^{13}C$ values in salmon from the River Frome ($R^2 = 0.11$, $p < 0.001$), see Fig. 3.3b. This negative relationship between $\delta^{13}C$ values and mass is contrary to what would be expected if $\delta^{13}C$ values were controlled by trophic level (DeNiro & Epstein 1978), with the smaller fish having heavier $\delta^{13}C$ values relative to the larger MSW fish. There is no significant relationship, however between mass and $\delta^{13}C$ values in salmon from the Northeast Coast, see Fig. 3.4b. The observed patterns, or lack thereof, for mass and carbon isotopes in these populations strongly suggest that factors other than trophic status have the greatest influence on $\delta^{13}C$ values in these fish. As discussed in section 3.3 $\delta^{13}C$ values in marine megafaunal tissues have been found to relate strongly to foraging habitat baseline $\delta^{13}C$ values, often with isotopic separation seen between migration start and end points and separate feeding populations (Cherel et al. 2009; Hobson & Schell 1998; Lee et al. 2005). The results from the regressions between body mass and $\delta^{13}C$ values indicated that $\delta^{13}C$ values should not be corrected for mass effects in either population. As these $\delta^{13}C$ values do not appear to be controlled by mass, and therefore trophic level, variations are likely due to variability in ecosystem baseline values (Barnes et al. 2009; Lara et al. 2010; Laws et al. 1995; Rau et al. 1996; Rau et al. 1989). It is thus possible that there is a relationship between mass and location, with River Frome MSW fish feeding in an area or areas with lower basal $\delta^{13}C$ values than River Frome grilse, and Northeast Coast salmon all feeding under similar baseline $\delta^{13}C$ conditions, likely in similar areas.

3.5. Correction for mass

Scale $\delta^{15}N$ values, for both River Frome and Northeast Coast salmon, were corrected for the observed mass effects to investigate variations in $\delta^{15}N$ values that may reflect the relative isotopic baseline of their feeding grounds. This correction was carried out using the following equation:

$$y_{corr} = \left(\frac{y_{meas}}{y_{calc}} \right) y_{mean}$$

Where y_{corr} is mass corrected isotopic value, y_{meas} is the initial isotope measurement value, y_{calc} denotes the expected isotopic value for the body mass of that fish given the regression coefficient from the relationships shown in Figs. 3.3a & 3.4a (1.91 for the River Frome and 0.84 for the Northeast Coast) (m (Ln(x)) + c) and y_{mean} denotes calculated isotopic ratio for the mean body mass value of the cohort (m (Ln($\bar{x}$)) + c). An overall summary of these data, both original and mass corrected, is shown below in Table 3.4.

Table 3.4. Summary of results from all analyses for δ^{13}C and δ^{15}N values, uncorrected and mass corrected (‰), on River Frome and Northeast Coast archive salmon scales.

Cohort	**n**	**Mean δ^{13}C value ‰ (±SD)**	**Mean uncorrected δ^{15}N value ‰ (±SD)**	**Mean mass corrected δ^{15}N value ‰ (±SD)**
RF All	324	-16.2 ±0.58	10.4 ±1.13	10.6 ±0.85
RF Grilse	183	-16.0 ±0.54	9.8 ±1.04	9.8 ±0.90
RF MSW	141	-16.5 ±0.48	11.2 ±0.73	11.2 ±0.68
NEC All	283	-15.5 ±0.81	10.1 ±1.23	10.2 ±0.84
NEC Grilse	142	-15.6 ±0.79	9.7 ±1.11	10.1 ±0.97
NEC MSW	141	-15.5 ±0.83	10.5 ±0.76	10.3 ±0.63

As shown in Table 3.4, mass correction slightly reduces the δ^{15}N variation for both populations and in both cohorts. The corrected δ^{15}N values for grilse and MSW salmon were compared by ANOVA, and found to remain significantly different for the River Frome cohorts ($F = 208.54$, $p < 0.001$), but were no longer significantly different for the Northeast Coast cohorts ($F = 3.43$, $p = 0.066$).

Fig. 3.5 shows the δ^{15}N: δ^{13}C ratio data for a) the River Frome and b) the Northeast Coast after the δ^{15}N values have been corrected for mass effects (hereafter termed δ^{15}N'). These plots should, therefore, show the effects of baseline differences, or absolute trophic level differences, in δ^{15}N and δ^{13}C values, independent of any mass effects. Clear separation remains in both δ^{13}C and δ^{15}N' values between grilse and MSW fish from the River Frome stock. MSW fish are elevated in δ^{15}N' but depleted in δ^{13}C values relative to grilse, which suggests either that there is an overall trophic level separation and/or that there is a regional baseline effect controlling δ^{15}N' values. In Pacific tuna, Graham et al. (2010) found that trophic level and baseline ecosystem δ^{15}N value effects combined to determine tissue δ^{15}N values, with a total δ^{15}N variation of 12 – 14 ‰. As the observed range in diet was small compared to the high isotopic variation (which would otherwise equate to approximately 4 – 5 trophic levels), the majority of the variation in tissue δ^{15}N values must stem from the tuna feeding in spatially discrete areas of the ocean. Similar results were also found by Jennings & Warr (2003), where between 51 and 77 % of variation in fish tissue δ^{15}N values was explained by variation in baseline δ^{15}N values. In contrast, there is no significant separation between δ^{15}N' values for Northeast Coast grilse and MSW salmon, which suggests that these fish experience very similar baseline δ^{15}N conditions, with the separation in pre-mass correction δ^{15}N values between the cohorts likely due to trophic level differences.

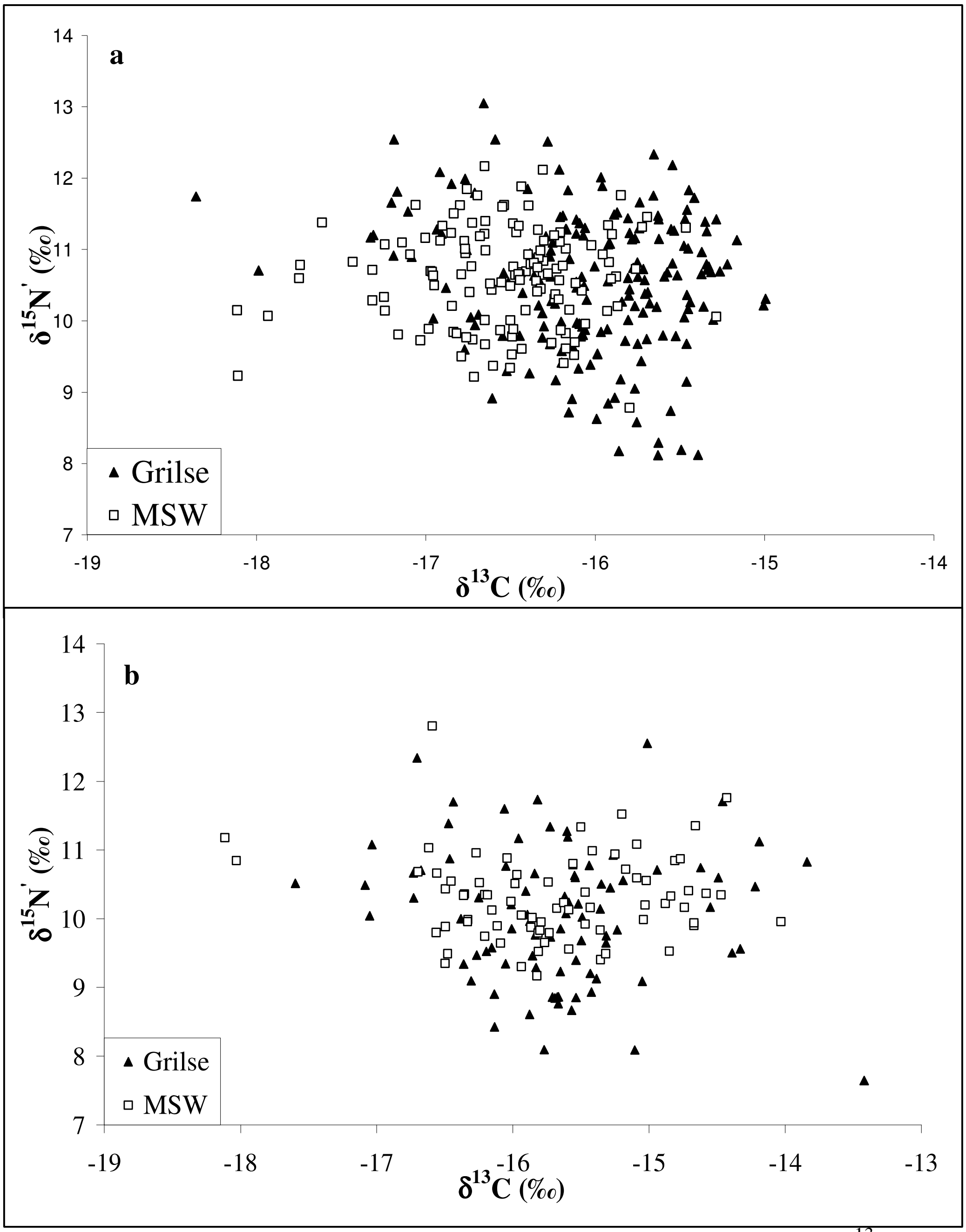


Figure 3.5. Scatter plot of results from analyses to date of archive scales for δ^{13}C and mass corrected δ^{15}N (δ^{15}N') values for a) River Frome salmon and b) Northeast Coast salmon (outliers noted above removed).

3.6. Baseline $\delta^{15}N$ differences between grilse and MSW fish

It was hypothesised that there would be no baseline variation in $\delta^{15}N'$ values between populations or cohorts, as all fish are thought to feed in a mixed stock in the northeast Atlantic (Holm et al. 2003). ANOVA results comparing mass corrected grilse and MSW $\delta^{15}N$ values for both populations are shown in Table 3.5. This mixed stock hypothesis is not supported for any of the cohorts, with the exception of the Northeast Coast grilse and MSW fish, which seem to experience similar baseline $\delta^{15}N$ conditions. All other cohorts, when compared, appear to be experiencing significantly different baseline ecosystem conditions in both $^{15}N'$ and ^{13}C, see Tables 3.3 and 3.5, indicating oceanographic separation between each cohort apart from those of the Northeast Coast.

Table 3.5. Results of ANOVA on $\delta^{15}N'$ values between cohorts from the River Frome and the Northeast Coast.

ANOVA	**n**	**F**	**p**
$\delta^{15}N'$ River Frome Grilse vs MSW	183, 141	208.54	**<0.001**
$\delta^{15}N'$ Northeast Coast Grilse vs MSW	86, 75	3.43	0.066
$\delta^{15}N'$ River Frome Grilse vs Northeast Coast Grilse	183, 86	4.28	**0.039**
$\delta^{15}N'$ River Frome MSW vs Northeast Coast MSW	141, 75	82.42	**<0.001**
$\delta^{15}N'$ River Frome Grilse vs Northeast Coast MSW	183, 75	17.86	**<0.001**
$\delta^{15}N'$ River Frome MSW vs Northeast Coast Grilse	141, 86	100.31	**<0.001**

3.7. Isotopic separation

The $\delta^{13}C$ and $\delta^{15}N$ results discussed above can be used to test hypotheses 1 to 3 of this thesis.

- Firstly, that there is trophic separation between the cohorts in both populations. There is demonstrated separation in $\delta^{15}N$ values between the cohorts, with the larger MSW fish showing consistently higher $\delta^{15}N$ values than the smaller grilse. This is corroborated through the population-wide increase in $\delta^{15}N$ values with mass, the reduction of variation in $\delta^{15}N$ values after correction for mass effects, and the removal of separation in $\delta^{15}N$ values between the Northeast Coast cohorts after correction for mass.

- Secondly, that salmon from different English populations feed in a common area in the season prior to return. The results discussed above show significant differences between all cohorts and populations in both $\delta^{13}C$ and $\delta^{15}N'$ values (taken as a proxy for baseline $\delta^{15}N$ values) with the exception of the Northeast Coast cohorts, which do not experience significantly different conditions to one another in either isotope. This result demonstrates that there is separation in marine feeding areas between each cohort from the River Frome, and between the River Frome cohorts and the Northeast Coast population, but not between Northeast Coast grilse and MSW fish, which appear to occupy similar feeding grounds, In conclusion, not all English salmon stocks share a common North Atlantic feeding ground (e.g. Faroe Islands or west of Greenland).

- Thirdly, that grilse and MSW salmon from the same natal origin feed in different areas in the season prior to return. For the River Frome, the baseline isotopic values of $\delta^{13}C$ and $\delta^{15}N'$ are indeed different, indicating that grilse and MSW salmon from this population do feed in separate locations prior to return. This was not, however, found for the Northeast Coast, where the $\delta^{13}C$ and $\delta^{15}N'$ values were not significantly different between the cohorts, indicating that these fish occupy similar marine feeding in the season prior to their return migration. Based on these results, it appears that both population and cohort membership determine the level of mixing within each stock.

3.8. Comparison with other Atlantic salmon scale isotope values

In order to test the fourth hypothesis, that salmon from English populations share feeding grounds with grilse from Newfoundland, River Frome and Northeast Coast isotope data were compared with data on grilse returning to Canada in a published study by Sinnatamby et al. (2009). The Canadian fish analysed most likely occupied feeding grounds in the Labrador Sea to the west of Greenland during their last growth season prior to return. This study investigated $\delta^{13}C$ and $\delta^{15}N$ values of scale collagen from grilse originating in nine Canadian rivers. It must be noted, however, that scales used in the Sinnatamby et al. (2009) study were subject to a different dissection protocol, using the entire marine portion of the scale for analysis; all comparative interpretations must, therefore be made with caution as a large portion of the out-migration and first year at sea will be integrated in the isotope values.

Data from all Canadian rivers in the Sinnatamby dataset were combined due to the low inherent variability in their isotopic data, and compared with isotope data for grilse and MSW salmon from the Frome and Northeast Coast, see Table 3.6 below. Results of these comparisons are given below in Table 3.7. The Canadian fish, when taken as a group, show significantly less variation than Frome and Northeast Coast grilse in both uncorrected and mass corrected δ^{15}N values, significantly greater variation than Frome and Northeast Coast MSW in mass corrected δ^{15}N' values, and no significant difference in variation between Frome and Northeast Coast MSW in uncorrected δ^{15}N values. The higher δ^{15}N variation in grilse from both UK populations for both uncorrected and mass corrected values indicates that these cohorts experience more variable trophic and baseline δ^{15}N conditions at sea than the entire variation experienced by the Canadian stocks. Alternatively, and more likely, the low variation in the Canadian stocks may reflect sampling differences, as the Canadian fish are sampled over the entire marine feeding period, thus retuning values of average diet conditions for each fish over its entire marine mass range. The UK MSW cohorts, in contrast, appear to experience similar levels of trophic variability, but significantly less ecosystem baseline δ^{15}N variability, although it would be necessary to correct the Canadian data for mass effects in order to further elucidate this result.

These Canadian stocks, again taken as a whole group, showed significantly less variability in δ^{13}C values compared to both UK grilse and MSW salmon. The results of these tests on the δ^{13}C data suggest that Frome salmon from both cohorts experienced higher levels of variability in ocean climate conditions to the Sinnatamby fish, also suggesting, conversely, that the Canadian fish occupy feeding grounds with relatively stable climatic conditions.

Comparisons of data from the Frome and the Sinnatamby et al. (2009) study suggest that Canadian grilse feed at a higher trophic level, or in more productive systems than all UK grilse and MSW salmon, both uncorrected and mass-corrected, analysed here, or that they experience different baseline ecosystem δ^{15}N conditions, see Table 3.7. The

Sinnatamby fish were also found to be significantly more depleted in ^{13}C than all UK cohorts with the exception of the MSW fish from the Frome, indicating that Canadian and UK populations analysed here, on average, experience different climatic conditions. According to the overall gradient of $\delta^{13}C$ values in the North Atlantic (Graham et al. 2010; Hofmann et al. 2000), the River Frome MSW fish potentially experienced the coolest conditions, followed by the Canadian fish, then the River Frome grilse, while the Northeast Coast salmon potentially fed in warmer waters on their feeding grounds.

The majority of these Sinnatamby data are from populations of salmon stemming from rivers restricted to Newfoundland, that enter the sea in similar areas and into the same ocean currents, and are therefore likely to be in similar places during post-smolt feeding, i.e. the Labrador Sea. If the UK fish analysed here were using feeding grounds to the west of Greenland in the Labrador Sea, they would be expected to integrate similar values of $\delta^{13}C$ to those seen in the Canadian stocks. As the UK $\delta^{13}C$ values are significantly different in each population and cohort to the Sinnatamby values, the fourth thesis hypothesis, that salmon from English populations share feeding grounds with grilse from Newfoundland, may be rejected, which also leads to rejection of the theory that either grilse or MSW returning English fish analysed here are feeding to the west of Greenland.

Table 3.6. Comparative summary of $\delta^{13}C$ and $\delta^{15}N$ scale data from the River Frome and Northeast Coast and a study on grilse from 9 Canadian rivers (Sinnatamby et al. 2009); all fish analysed for the Sinnatamby dataset were grilse.

Region	**River (cohort)**	**n**	**Mean $\delta^{15}N$**	**$\delta^{15}N$ SD**	**Mean $\delta^{15}N'$**	**$\delta^{15}N'$ SD**	**Mean $\delta^{13}C$**	**$\delta^{13}C$ SD**
All Sinnatamby et al. (2009) Canadian data	-	702	11.7	0.83	n/a	n/a	-16.2	0.35
Gulf of St Lawrence	Miramichi	339	11.3	0.46	n/a	n/a	-16.1	0.32
	Restigouche	330	11.5	0.49	n/a	n/a	-16.0	0.31
	De la Trinité	247	12.5	0.55	n/a	n/a	-16.2	0.25
South Newfoundland	Northeast Placentia	194	11.3	0.53	n/a	n/a	-16.0	0.39
	Conne	196	11.8	0.43	n/a	n/a	-16.2	0.28
West Newfoundland	Humber	110	11.5	0.56	n/a	n/a	-15.8	0.32
	Western Arm Brook	294	11.1	0.50	n/a	n/a	-16.2	0.42
Northeast Newfoundland	Gander	257	11.1	0.64	n/a	n/a	-16.2	0.42
	Terra Nova	199	11.2	0.62	n/a	n/a	-16.0	0.31
UK	River Frome (grilse)	183	9.8	1.07	9.8	0.94	-16.0	0.54
	River Frome (MSW)	141	11.2	0.73	11.2	0.68	-16.5	0.48
	Northeast Coast (grilse)	142	9.7	1.11	10.1	0.97	-15.6	0.79
	Northeast Coast (MSW)	141	10.5	0.76	10.3	0.63	-15.5	0.83

Table 3.7. Results of comparative tests for δ^{13}C and δ^{15}N data from the River Frome, Northeast Coast and Sinnatamby datasets; bold denotes $\alpha \leq 0.05$.

Test	Comparisons	n	Isotope	F	W	p
F test	Frome grilse: Sinnatamby	183: 702	δ^{15}N	1.69	-	**<0.001**
		180: 702	δ^{15}N’	1.49	-	**<0.001**
	Frome MSW: Sinnatamby	141: 702	δ^{15}N	0.79	-	0.08
		130: 702	δ^{15}N’	0.68	-	**0.007**
Levene’s test	Frome grilse: Sinnatamby	183: 702	δ^{13}C	-	49.13	**<0.001**
	Frome MSW: Sinnatamby	141: 702	δ^{13}C	-	15.83	**<0.001**
	Frome grilse: NEC grilse	183, 142	δ^{13}C	-	15.00	**<0.001**
	Frome MSW: NEC MSW	141, 139	δ^{13}C	-	41.76	**<0.001**
F test	NEC grilse: Sinnatamby	142: 702	δ^{15}N	1.81	-	**<0.001**
		94: 702	δ^{15}N’	1.38	-	**0.03**
	NEC MSW: Sinnatamby	139: 702	δ^{15}N	0.83	-	0.19
		75: 702	δ^{15}N’	0.57	-	**0.003**
	Frome grilse: NEC grilse	183, 142	δ^{15}N	1.07	-	0.66
		180, 96	δ^{15}N’	0.93		0.71
	Frome MSW: NEC MSW	141, 139,	δ^{15}N	1.06	-	0.72
		130, 75	δ^{15}N’	1.28	-	0.43
Levene’s test	NEC grilse: Sinnatamby	142: 702	δ^{13}C	-	155.75	**<0.001**
	NEC MSW: Sinnatamby	139: 702	δ^{13}C	-	238.97	**<0.001**
ANOVA	Frome grilse: Sinnatamby	183: 702	δ^{15}N	653.78	-	**<0.001**
		180: 702	δ^{15}N’	254.00	-	**<0.001**
	Frome MSW: Sinnatamby	141: 702	δ^{15}N	47.98	-	**<0.001**
		130: 702	δ^{15}N’	188.72	-	**<0.001**
Mann-Whitney U test	Frome grilse: Sinnatamby	183: 702	δ^{13}C	-	98362	**<0.001**
	Frome MSW: Sinnatamby	141: 702	δ^{13}C	-	36750	**<0.001**
ANOVA	Northeast Coast grilse: Sinnatamby	142: 702	δ^{15}N	573.80	-	**<0.001**
		94: 702	δ^{15}N’	281.24	-	**<0.001**
	Northeast Coast MSW: Sinnatamby	139: 702	δ^{15}N	247.41	-	**<0.001**
		75: 702	δ^{15}N’	195.11	-	**<0.001**
Mann-Whitney U test	Northeast Coast grilse: Sinnatamby	142: 702	δ^{13}C	-	94290	**<0.001**
	Northeast Coast MSW: Sinnatamby	139: 702	δ^{13}C	-	85020	**<0.001**

4. Results and discussion – Temporal trends in isotope data

Atlantic salmon have been in decline since the 1970s, with a particular downturn in the early 1990s (e.g. Cowx & Van Zyll De Jong 2004; ICES 2009b), as detailed in the Introduction chapter. One of the primary aims of this thesis was to investigate the marine ecology of the Atlantic salmon through time in order to determine whether changes in ecology, e.g. trophic behaviour or feeding location, had occurred concurrently with the population downturn.

Isotopic $\delta^{13}C$, $\delta^{15}N$ and $\delta^{15}N'$ values for grilse and MSW salmon from the River Frome and Northeast Coast archives were averaged by year to investigate temporal trends in trophic level and marine conditions. The year of summer feeding was determined by the date of capture combined with the microscopically-read sea-age of each fish, as detailed in the Materials & Methods section. The results in Tables 4.1 and 4.2 are summary data for the last season of growth (summer) at sea, not necessarily the year of return, for salmon from the River Frome and Northeast Coast, respectively. The data shown are mean annual isotopic values with standard deviations (all outliers detailed in chapter 3 are excluded from analyses). Full results for each individual fish from each population are included in electronic Appendices B and C.

Table 4.1. Results from all analyses for $\delta^{13}C$, $\delta^{15}N$ and mass corrected $\delta^{15}N'$ values (‰) to date on River Frome archive salmon scales by year analysed (last summer season of growth). Isotope values are ‰, ± 1 standard deviation.

Year	Grilse (n)	Mean $\delta^{13}C$ value	Mean $\delta^{15}N$ value	Mean $\delta^{15}N'$ value	MSW (n)	Mean $\delta^{13}C$ value	Mean $\delta^{15}N$ value	Mean $\delta^{15}N'$ value
1971	3	-16.5 ±0.31	9.3 ±0.68	9.9 ±1.22				
1972					1	-15.9	10.4	10.2
1979					7	-16.5 ±0.14	11.3 ±0.91	10.8 ±1.04
1980	3	-16.4 ±0.14	11.2 ±0.42	10.9 ±0.32	10	-16.2 ±0.08	11.1 ±0.68	10.3 ±0.58
1981	9	-15.8 ±0.69	9.9 ±0.86	10.3 ±0.52	5	-16.0 ±0.09	11.3 ±0.82	10.9 ±0.33
1982	2	-15.6	9.7	10.4	10	-16.7 ±0.20	11.4 ±0.74	10.4 ±0.49
1983	10	-16.1 ±0.35	8.9 ±0.62	9.4 ±0.38	9	-16.8 ±0.23	10.8 ±0.68	10.6 ±0.64
1984	10	-16.2 ±0.46	9.9 ±1.33	10.1 ±1.14	10	-16.9 ±0.17	11.0 ±0.69	10.4 ±0.48
1985	10	-16.2 ±0.50	10.2 ±0.84	10.6 ±0.61	10	-16.9 ±0.16	11.3 ±0.77	10.7 ±0.82
1986	10	-16.2 ±0.43	9.9 ±0.52	10.7 ±0.69	10	-16.4 ±0.07	11.1 ±0.71	10.9 ±0.79
1987	10	-15.8 ±0.83	10.2 ±0.63	10.9 ±0.48	10	-16.4 ±0.08	11.3 ±0.63	10.5 ±0.70
1988	10	-15.6 ±0.32	10.0 ±0.70	10.9 ±0.70	10	-16.6 ±0.07	11.5 ±0.60	11.1 ±0.78
1989	10	-16.4 ±0.53	10.6 ±0.90	11.0 ±0.68	1	-15.9	10.9	10.6
1990	8	-15.7 ±0.46	10.1 ±0.89	10.9 ±0.68	6	-16.5 ±0.16	11.8 ±0.55	10.9 ±0.66
1991	1	-16.1	9.6	10.6	5	-16.5 ±0.08	11.3 ±0.54	10.9 ±0.28
1992	6	-16.0 ±0.43	10.0 ±0.40	11.0 ±0.71	6	-16.0 ±0.16	10.4 ±0.28	10.1 ±0.28
1993	9	-15.9 ±0.59	9.9 ±0.67	10.8 ±0.54	1	-15.8	11.0	10.7
1994	8	-15.6 ±0.23	9.5 ±1.57	10.1 ±1.52	7	-16.5 ±0.25	10.8 ±1.09	10.4 ±0.85
1995	10	-15.8 ±0.36	9.6 ±0.74	10.6 ±0.75				
1996	12	-16.0 ±0.35	9.2 ±1.01	10.1 ±0.90	8	-16.6 ±0.09	10.8 ±0.54	10.5 ±0.54
1997	7	-16.3 ±0.95	10.5 ±0.82	10.9 ±0.73	5	-16.6 ±0.34	11.0 ±0.64	10.6 ±0.82
1998	12	-16.0 ±0.44	9.0 ±1.25	10.1 ±1.41				
1999	7	-16.2 ±0.49	9.1 ±1.14	10.4 ±1.24				
2000					8	-16.7 ±0.11	11.3 ±0.68	10.6 ±0.88
2001	10	-16.4 ±0.53	10.1 ±1.64	10.6 ±1.32	2	-17.2	12.6	11.6
2002	5	-16.0 ±0.33	10.4 ±0.49	11.5 ±0.74				

Table 4.2. Results from all analyses for δ^{13}C, δ^{15}N and mass corrected δ^{15}N' values (‰) to date on Northeast Coast archive salmon scales by year analysed (last summer season of growth). Isotope values are ‰, ± 1 standard deviation.

Year	**Grilse (n)**	**Mean δ^{13}C value**	**Mean δ^{15}N value**	**Mean δ^{15}N' value**	**MSW (n)**	**Mean δ^{13}C value**	**Mean δ^{15}N value**	**Mean δ^{15}N' value**
1985	10	-16.2 ±0.90	11.7 ±0.81		8	-15.4 ±0.80	10.9 ±0.54	10.0 ±0.28
1986	2	-15.6	11.5		8	-14.9 ±0.89	10.1 ±1.25	
1987	12	-15.1 ±0.86	9.6 ±0.75	9.5	24	-15.0 ±0.37	10.7 ±0.70	10.6 ±0.56
1988	14	-14.6 ±0.62	9.8 ±0.99	10.3 ±0.99	9	-14.7 ±0.64	10.3 ±0.99	10.5 ±0.89
1989	16	-15.7 ±0.78	9.7 ±1.01	10.8 ±0.57	16	-15.5 ±0.90	10.6 ±0.61	10.3 ±0.61
1990	10	-15.5 ±0.34	10.2 ±1.06	10.3 ±0.97	9	-16.5 ±0.67	10.7 ±0.51	10.5 ±0.47
1991	10	-15.8±0.47	9.6 ±0.70	10.0 ±0.76	10	-16.7 ±0.49	11.2 ±0.55	
1992	10	-16.2 ±0.61	10.1 ±0.72	10.1 ±0.73	11	-16.0 ±0.38	10.2 ±0.48	9.9 ±0.47
1993	10	-15.9 ±0.40	9.2 ±0.68	9.4 ±0.74	5	-14.9 ±0.31	10.3 ±0.95	
1994	9	-15.7 ±0.56	8.8 ±0.86		6	-14.9 ±0.34	10.1 ±0.74	
1995	10	-14.8 ±0.45	8.9 ±0.94		20	-15.5 ±0.53	10.1 ±0.49	9.9 ±0.31
1996	9	-16.0 ±0.55	9.8 ±0.95	10.2 ±0.95	10	-15.9 ±0.70	10.4 ±1.02	10.6 ±1.27
1997	10	-15.8 ±0.61	9.6 ±0.77	9.8 ±0.83				
2000					3	-16.3 ±0.30	10.7 ±0.29	10.4 ±0.28
2001	18	-15.5 ±0.80	9.4 ±1.11	9.7 ±1.31				

4.1. Temporal δ^{13}C data

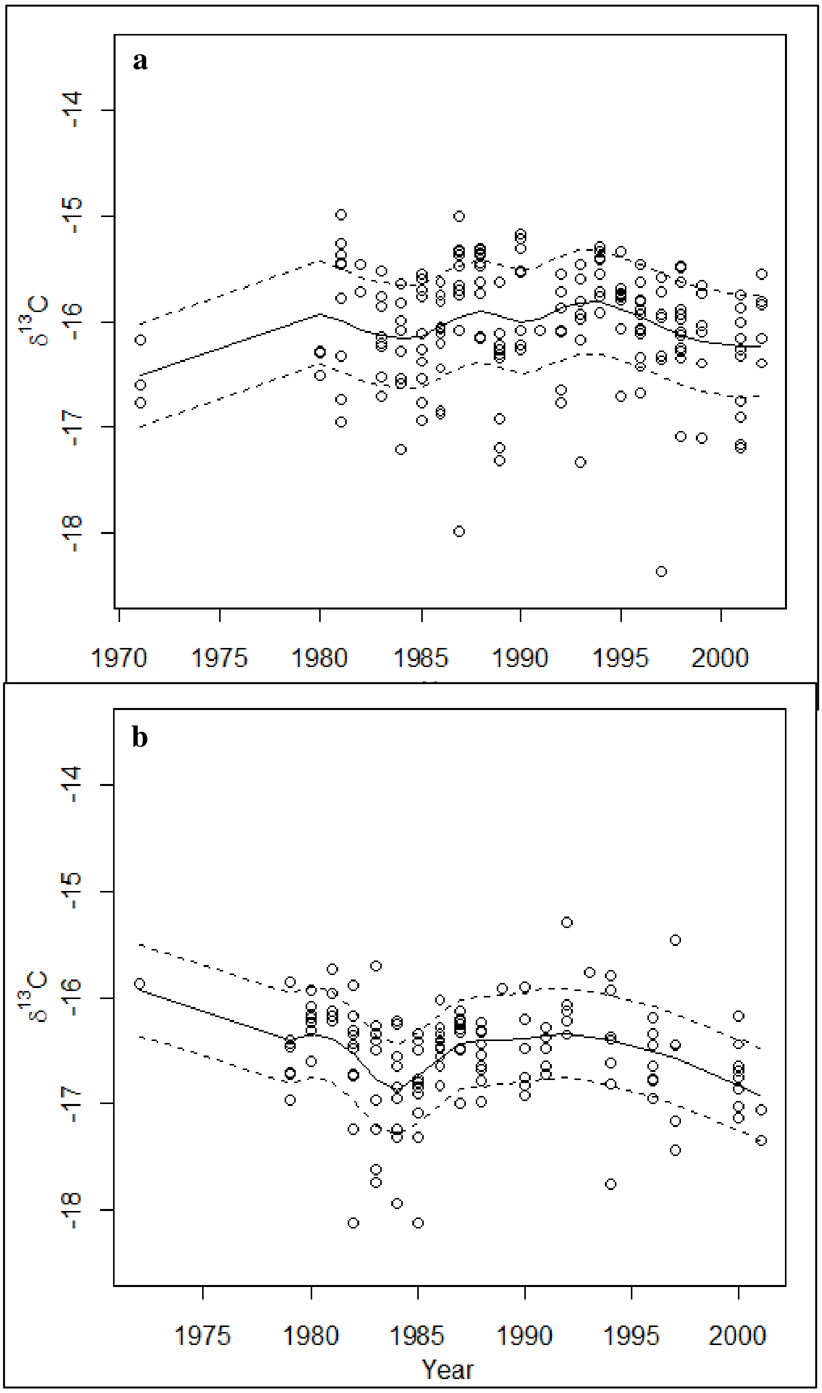


Figure 4.1. δ^{13}C values (‰) per year from a) River Frome grilse, and b) River Frome MSW fish between 1971 and 2002. The solid lines are second-order LOESS fits with a span width of 0.5; dashed lines show ± standard error of the residuals of the smoothed fit.

The δ^{13}C data for the River Frome archive show no clear patterns or trends over time for either grilse or MSW salmon, see Fig. 4.1a&b, and are relatively stable compared to the Northeast Coast cohorts (see below). The lack of trends in these data suggest that there have been no long term, directional changes in oceanic conditions for either cohort from this archive. As with the δ^{15}N data, there is a largely consistent separation in isotope ratios between the two cohorts, which is temporally maintained overall; this is unlikely to be due to trophic enrichment as the larger MSW fish are isotopically depleted compared to the smaller grilse.

The mechanisms controlling δ^{13}C values in scale collagen are, as discussed in section 1.4, largely controlled by SST; this means that two very important conclusions may be reached from the δ^{13}C values of salmon from the River Frome through time:

> 1. Grilse and MSW salmon maintain separation in marine location in at least 12 of the 18 years for which both MSW and grilse data are available;
>
> and
>
> 2. Oceanic conditions, in terms of SST, are relatively stable through time in both areas used as feeding grounds by River Frome salmon, with the isotopically lighter values in the MSW fish possibly implying that they are feeding in cooler waters than the grilse, according to the latitudinal gradient of baseline δ^{13}C values (Best & Schell 1996; Hofmann et al. 2000; Kroopnick 1980; Lara et al. 2010).

Points 1 and 2, when combined, strongly suggest that grilse and MSW salmon from the River Frome consistently feed in different areas. It is theoretically possible that the fish are not feeding in the same regions consistently and are widely spread out in the Atlantic, but despite the large variation in plankton δ^{13}C values across the North Atlantic Ocean (Behrenfeld et al. 2006; Jaeger et al. 2010), the mean variance in salmon scale collagen δ^{13}C values within individual years is significantly less than the total variance (see Fig. 4.1a&b, ANOVA: RF 1SW, n = 145, df = 16, F = 2.5, $p < 0.01$, RF MSW n = 88, df = 13, F = 2.7, $p<0.01$). These results indicate that, in each sampled year, returning salmon within each age group fed in a common location. It is also possible that the low variance in scale δ^{13}C values is the result of a highly migratory life history while at sea, producing averaged mean values. The low within-year variability coupled with the inter-annual stability seen in Fig. 4.1a&b, however, would require that both cohorts would have to not only track areas of sea with similar temperature and primary productivity regimes, but also that they would have to undertake this tracking as two cohort groups, each group with individual condition preferences, for this migratory hypothesis to hold true. It is much more likely that each cohort migrates year on year to traditional feeding grounds, one for MSW fish and one for grilse. Given the lack of temporal variation in scale $\delta^{13}C$ values for either grilse or MSW salmon, it is also reasonable to conclude that these feeding grounds maintain relatively stable SSTs throughout the years covered by these analyses. In order to test for long term repeating patterns and relationships in the time series data, auto-correlation and cross-correlation analyses were run. Auto-correlation is correlation calculated between a series of data and itself with a lag; high correlations suggest signal periodicity of the lagged time duration (Bourke 1996). Cross-correlation is the same, but calculated between two series of data.

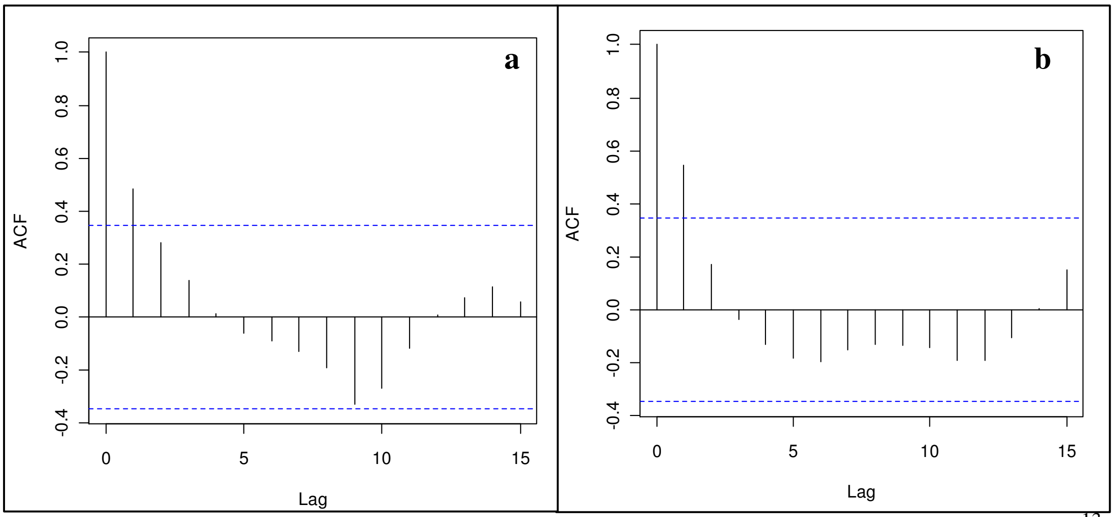


Figure 4.2. Correlograms showing autocorrelation (ACF) of the LOESS smoothed $\delta^{13}C$ value time series for a) River Frome grilse and b) River Frome MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The time series of scale $\delta^{13}C$ data show strong autocorrelation (Fig. 4.2) The grilse $\delta^{13}C$ data, show cyclical fluctuations with a return period of around 14 years. The MSW $\delta^{13}C$ data show weaker sinusoidal autocorrelation structure then seen in the grilse, with the possibility of a longer return period. The strong patterns of autocorrelation within these data suggest continuity in the mechanisms controlling the $\delta^{13}C$ data, most likely in the temperatures on the feeding grounds.

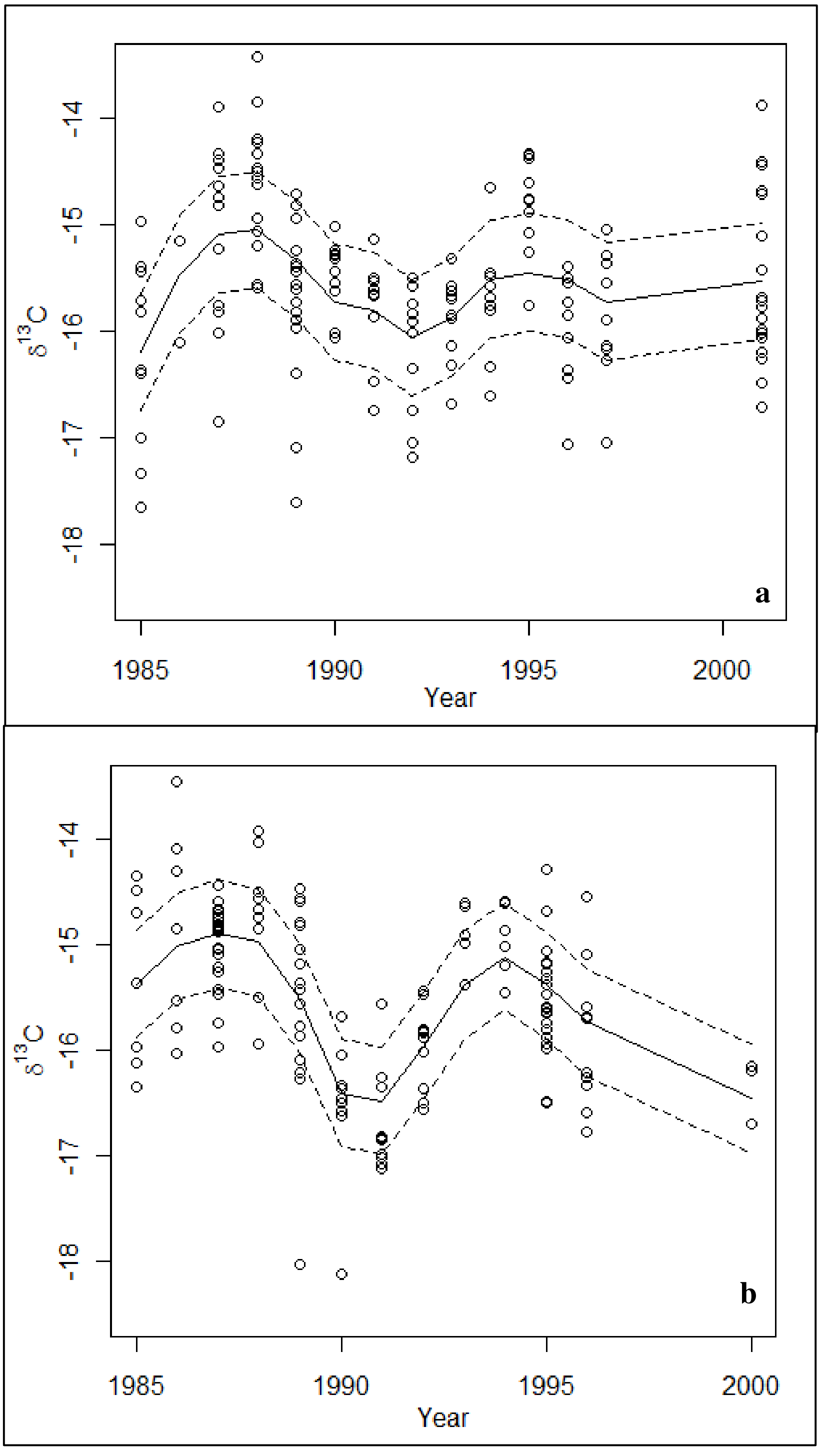


Figure 4.3. $\delta^{13}C$ values (‰) per year from a) Northeast Coast grilse and b) Northeast Coast MSW fish between 1985 and 2001. The solid lines are second-order LOESS fits with a span width of 0.5; dashed lines show ± standard error of the residuals of the smoothed fit.

As with the River Frome, the $\delta^{13}C$ data for the Northeast Coast driftnet archive also show no linear trends over time, although there are clear signs of multi-year oscillations (with an apparent period of approximately 6-9 years) in both sea age cohorts, see Fig. 4.3a&b. This suggests that there have been no long term, directional changes in oceanic conditions for either cohort from this archive, but the clear multi-year trends strongly suggest a long term (possibly climatic) influence on basal C values. There is a largely consistent overlap in isotope ratios between the two cohorts, which is, in general, temporally maintained. This overlap is unlikely to be trophically mediated as there is no significant difference in δ^{13}C values between larger MSW fish and smaller grilse, as shown in Table 3.2. The total variation in both cohorts of the Northeast Coast population is relatively high (grilse SD = 0.79, MSW SD = 0.83, see Table 4.2) compared to the within year variation (see Fig. 4.3, ANOVA: NEC 1SW n = 150, df=16, F=6.0, $p<0.001$; NEC MSW n =139, df = 12, F = 10.7, $p<0.001$) and the total variation in each cohort of the River Frome salmon, see above.

As with the δ^{13}C data from the River Frome, some very important conclusions may be reached from the δ^{13}C values of salmon from the Northeast Coast through time, i.e.:

1. Grilse and MSW salmon feed in similar locations (or at least in locations with similar isotopic compositions) in at least 9 of the 13 years for which both MSW and grilse data are available;
2. Within year variation is much lower for both cohorts than total variation, suggesting that there is intra-cohort integrity;

and

3. Oceanic conditions in the area used as a feeding ground by Northeast Coast salmon are relatively variable through time compared to those in the River Frome stock feeding grounds.

Points 1 and 2, when combined, strongly suggest that salmon from the Northeast Coast, as with the Frome cohorts, consistently migrate to a common feeding ground.

Given the relatively high temporal variation in these δ^{13}C values for grilse and MSW salmon, it is reasonable to conclude that their feeding grounds are subject to variable SSTs throughout the years covered by these analyses.

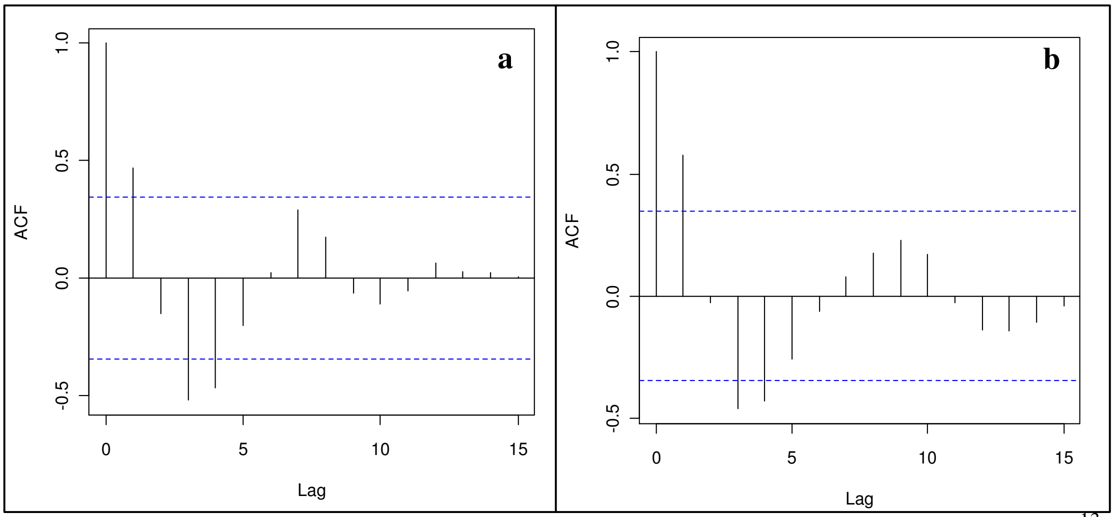


Figure 4.4. Correlograms showing autocorrelation (ACF) of the LOESS smoothed δ^{13}C value time series for a) Northeast Coast grilse and b) Northeast Coast MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

Time series of scale δ^{13}C values in both grilse and MSW salmon from the Northeast Coast show strong sinusoidal autocorrelation structure (Fig 4.4). Grilse δ^{13}C data display low frequency oscillations with a return period of around seven years. The MSW δ^{13}C data also show low frequency oscillations, with a return period of around nine years. The strong patterns of autocorrelation within these data again suggest continuity in the mechanisms controlling the δ^{13}C data, most likely in the temperatures on the feeding grounds, but with higher frequency oscillations for this Northeast Coast population than seen in the River Frome population. The higher frequency autocorrelations seen here echo the greater variability in the interannual δ^{13}C values (i.e. higher amplitude oscillations) than seen in the River Frome fish.

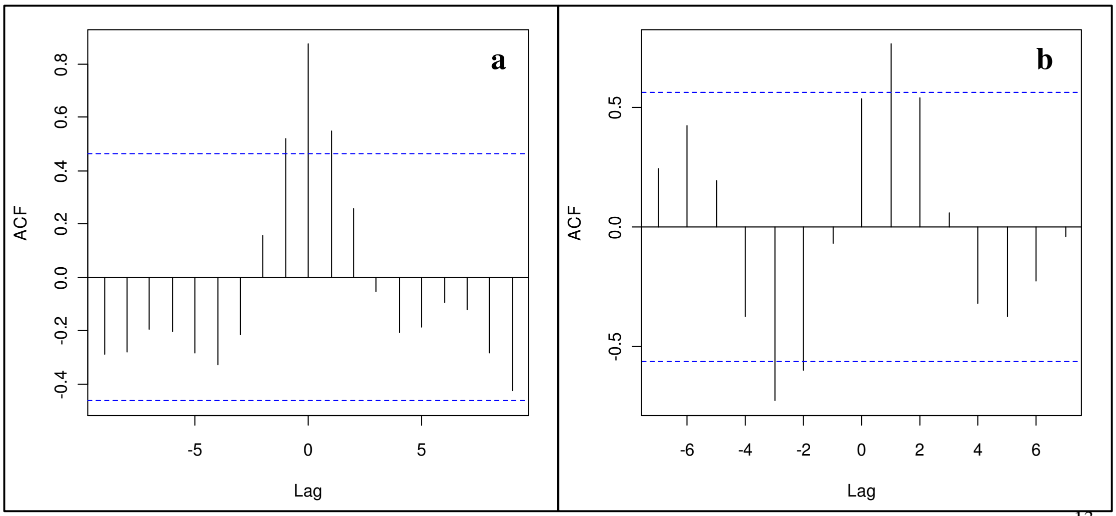


Figure 4.5. Correlograms showing cross-correlations (ACF) of the LOESS smoothed $\delta^{13}C$ value time series for a) RF grilse against RF MSW fish and b) NEC grilse against NEC MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The cross-correlation between $\delta^{13}C$ data in the River Frome cohorts (Fig. 4.5a) shows that grilse and MSW fish from this population are positively correlated at year zero, meaning that the temporal variations in each dataset are coincident, despite having different absolute $\delta^{13}C$ values in any single year. This suggests that, while these cohorts, are likely not feeding in the same exact feeding areas at sea, the two feeding areas are most probably subject to the same climatic influences, and are likely to be spatially associated. There is no apparent longer term relationship between the two time series. The Northeast Coast cohorts, in contrast, show a sinusoidal cross correlation structure, with highest positive cross correlations when MSW time series are lagged by one year relative to grilse. The oscillating nature of the cross correlations is a consequence of the strong sinusoidal autocorrelation structure of both time series. These cross-correlations imply that Northeast Coast grilse experience a given climatic condition one year after the MSW fish.

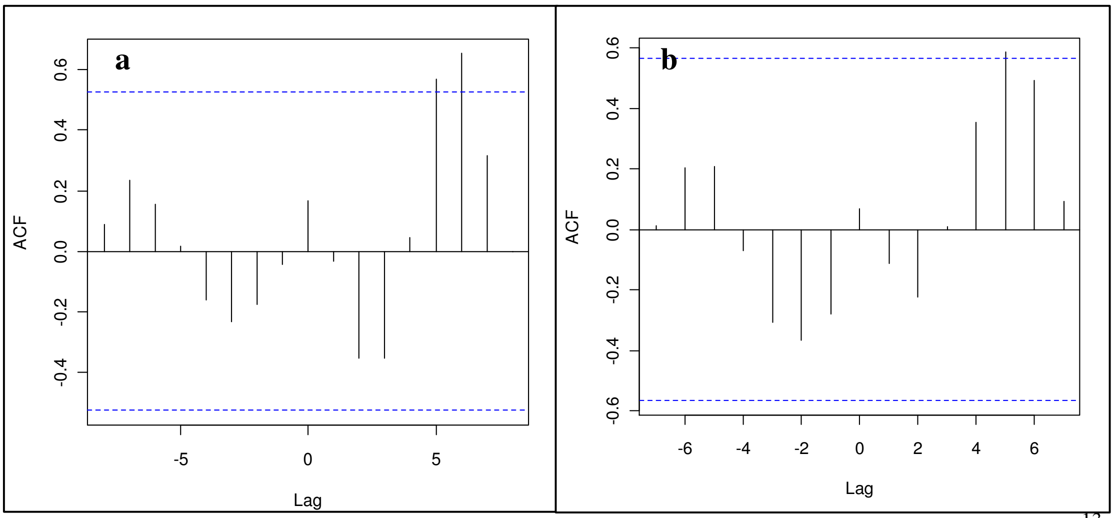


Figure 4.6. Correlograms showing cross-correlations (ACF) of the LOESS smoothed $\delta^{13}C$ value time series for a) RF grilse against NEC grilse and b) RF MSW fish against NEC MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The cross-correlations of $\delta^{13}C$ values between River Frome grilse and Northeast Coast grilse (Fig. 4.6a), and River Frome MSW fish and Northeast Coast MSW fish (Fig. 4.6b) show similar, but weak, patterns, possibly implying that climatic variables influencing $\delta^{13}C$ values are linked between the feeding grounds, but with the Northeast Coast feeding grounds preceeding those in the Frome feeding grounds by five to six years.

4.2. Temporal δ^{15}N and mass data

River Frome

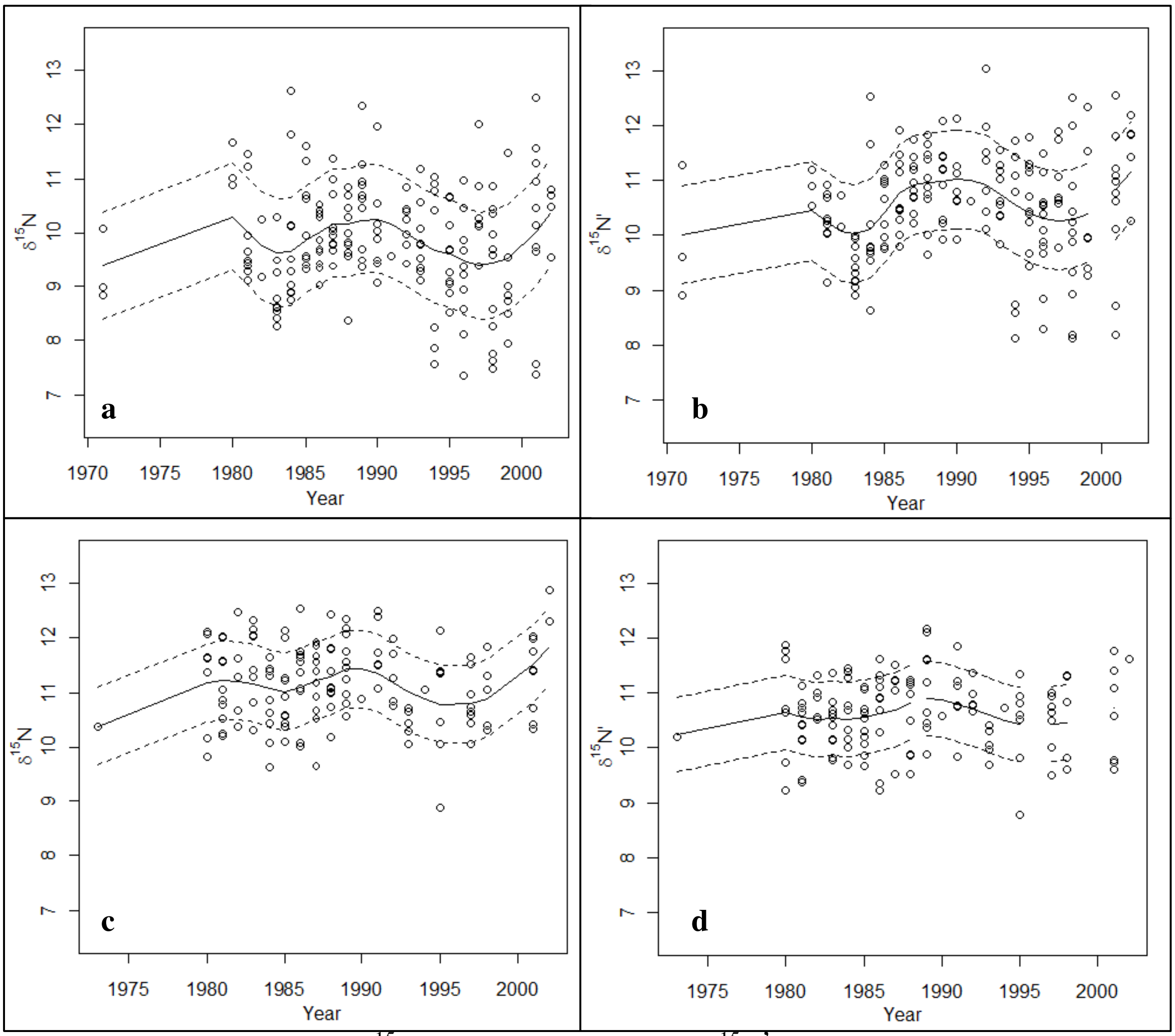


Figure 4.7. a) Uncorrected δ^{15}N and b) mass corrected δ^{15}N' values (‰) per year for River Frome grilse, and c) uncorrected δ^{15}N and d) mass corrected δ^{15}N' values (‰) per year for River Frome MSW fish between 1985 and 2002. The solid lines are second-order LOESS fits with a span width of 0.5; dashed lines show ± standard error of the residuals of the smoothed fit.

The δ^{15}N data for the River Frome archive show no significant, directional trends through time for either grilse or MSW salmon, see Fig. 4.7. For the uncorrected data, this suggests that there have been no long term, directional changes in trophic level for either cohort from this archive. From this result it may be concluded that the feeding grounds used by River Frome salmon are unlikely to have been subject to long-term directional change in ecosystem trophic structure. This result is contrary to what might have been suspected in many areas of the sea according to Pauly et al.'s (1998) research on "fishing down marine food webs", where preferential removal of larger fish through fishing reduced the overall trophic levels within marine ecosystems. The lack of trend in the mass corrected data suggests that there have been no directional changes in the baseline $\delta^{15}N$ values in the feeding grounds these fish inhabit at sea. There are, however, in both uncorrected and mass corrected data for grilse and MSW fish, signs of potential multi-year oscillations, which are investigated further below.

There is a significant difference in $\delta^{15}N$ compositions of grilse and MSW fish (as discussed above, and shown in Tables 3.2 and 3.5), which is clearly maintained in each year throughout the time covered by these analyses. While there is some level of variation in values between years for both cohorts, this variation is not directional. As the majority of the variation is also seen in mass corrected $\delta^{15}N$ values, it is likely that this variation reflects changes in the availability of preferred food types, i.e. larger, higher trophic level prey, or ecosystem baseline $\delta^{15}N$ values on an inter-annual basis (Best & Schell 1996; Graham et al. 2010; Tamelander et al. 2009).

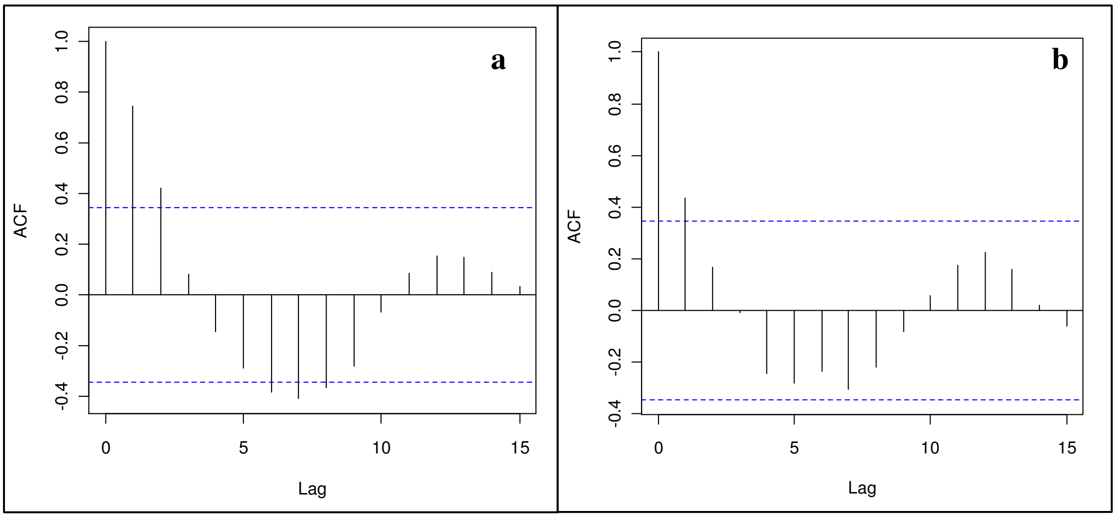


Figure 4.8. Correlograms showing autocorrelation (ACF) of the LOESS smoothed uncorrected $\delta^{15}N$ value time series for a) River Frome grilse and b) River Frome MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

Time series of both grilse and MSW salmon from the River Frome are strongly autocorrelated with similar, sinusoidal correlation structure (Fig. 4.8). Both data series show a return period of around 12 years. The strong autocorrelation within these data suggest non-random temporal behaviour in the mechanisms controlling the $\delta^{15}N$ data. These mechanisms may include trophic level changes due to ecosystem structure, e.g. the dynamics of abundance in preferred prey species such as herring (Haugland et al. 2006; Holst et al. 1998; ICES 2009a; Jacobsen & Hansen 2001), or basal ecosystem productivity dynamics (Hobson 1999; Jennings & Warr 2003; Lara et al. 2010; Rubenstein & Hobson 2004).

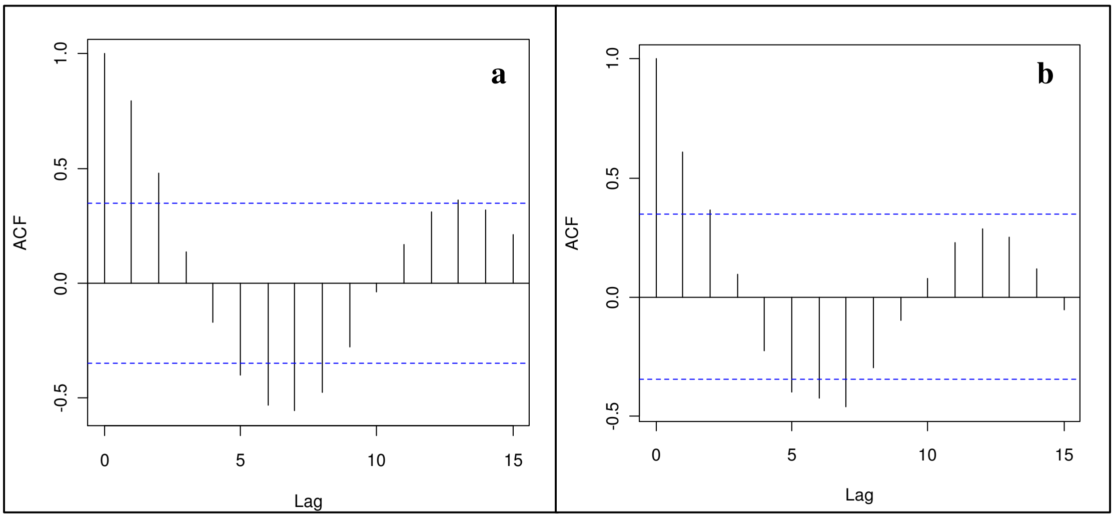


Figure 4.9. Correlograms showing autocorrelation (ACF) of the LOESS smoothed mass corrected $\delta^{15}N'$ value time series for a) River Frome grilse and b) River Frome MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

As Fig. 4.9 shows, the autocorrelation in the uncorrected $\delta^{15}N$ data from the River Frome cohorts (Fig. 4.8) is strengthened post-mass correction. The periodicity is the same for both uncorrected and mass corrected data, but the significance becomes higher for both cohorts in these corrected data. This strengthening suggests that the $\delta^{15}N$ values are controlled largely by ecosystem baseline variation and/or variation in preferred prey abundance (Lara et al. 2010; Vanderklift & Ponsard 2003). Future work should be carried out to better identify these causal mechanisms.

The ratio of measured (uncorrected) to expected (from the body mass and $\delta^{15}N$: mass relationship, as detailed in section 3.4) $\delta^{15}N$ values against time was plotted to investigate the possibility of long-term trophic level reduction, see Fig. 4.10. This ratio should be the mass-related and therefore trophic signal for each cohort taken from these data, separated from the baseline $\delta^{15}N$ signal.

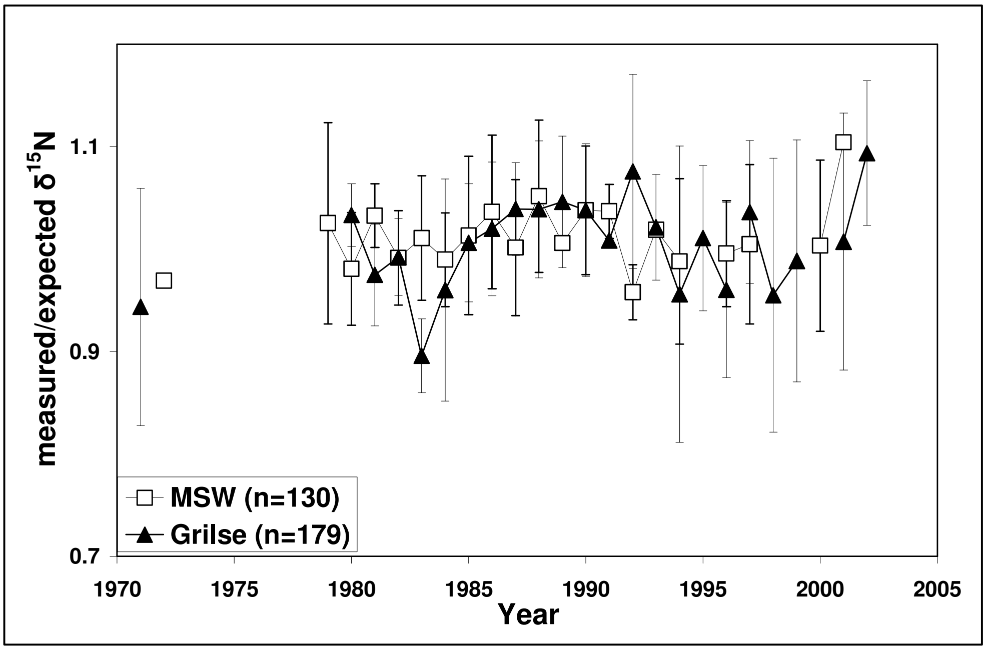


Figure 4.10. Ratio of mean measured: expected (based on mass) δ^{15}N values (‰) per year from the River Frome for grilse (filled triangles) and MSW fish (empty squares) between 1971 and 2002; error bars are ±1SD, means used for graphical clarity.

No significant directional trend in trophic signal is seen in either grilse or MSW salmon from the River Frome over time (see Fig. 4.10). While no trend in trophic level was observed, it has been suggested that salmon in some rivers have been reducing in size over time (Jonsson & Jonsson 2004a; Jonsson & Jonsson 2004b; Quinn et al. 2006; Welton et al. 1999). To test whether any temporal decline was apparent in the mass of the River Frome fish analysed here, annual mass of each fish sampled for both cohorts was plotted against time, shown in Fig. 4.11.

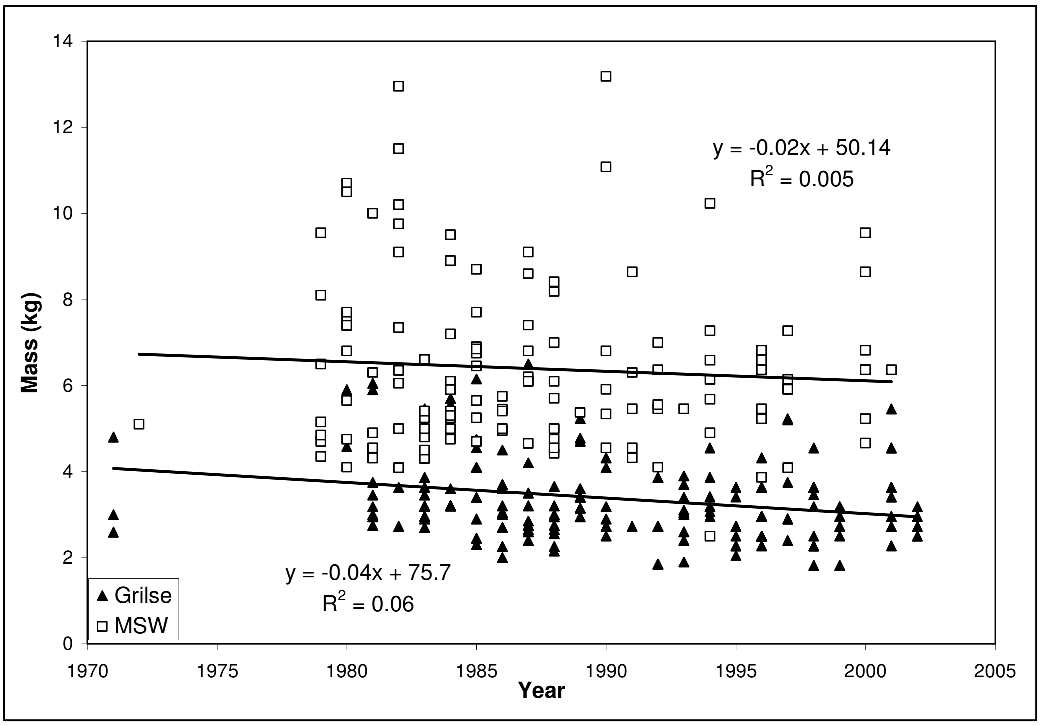


Figure 4.11. Mass (kg) per year from the River Frome for salmon sampled between 1971 and 2002; grilse are shown as filled triangles and MSW fish as empty squares.

There is no significant directional change in mass of the RF MSW salmon for the time covered by these analyses (see Fig. 4.11). A significant decline ($n = 180$, $R^2 = 0.06$, $p < 0.005$) is seen through time in the mass of the returning RF grilse, indicating that these fish are progressively becoming smaller. Welton et al (1999) also found a temporal decline in length of grilse returning to the Frome, based on photographic data, but, in contrast to the present study, they found an increase in length for MSW salmon from this population. It is possible that oceanic conditions for grilse are progressively becoming less favourable for growth over time. Shrinking grilse will have implications for the viable population size of the grilse-dominated River Frome, as smaller fish are relatively less fecund, producing fewer, smaller eggs (Fleming 1996; Garcia de Leaniz et al. 2007; Hendry et al. 2001), which may be an explanatory mechanism in the declining population size.

Northeast Coast

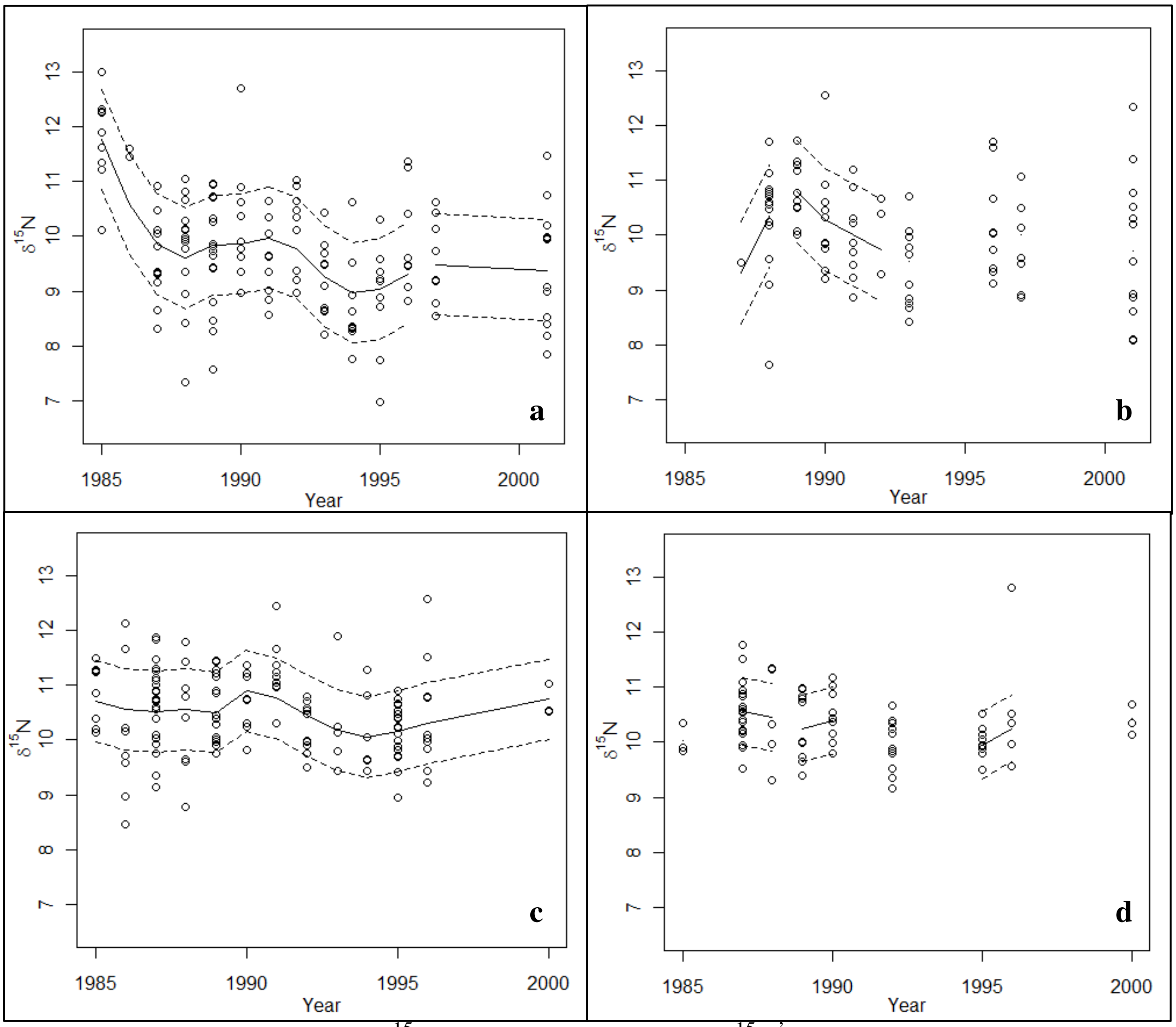


Figure 4.12. a) Uncorrected $\delta^{15}N$ and b) mass corrected $\delta^{15}N'$ values (‰) per year for Northeast Coast grilse, and c) uncorrected $\delta^{15}N$ and d) mass corrected $\delta^{15}N'$ values (‰) per year for Northeast Coast MSW fish between 1985 and 2002. The solid lines are second-order LOESS fits with a span width of 0.5; dashed lines show ± standard error of the residuals of the smoothed fit.

Annual $\delta^{15}N$ values in fish from the Northeast Coast populations are shown in Fig. 4.12. There was a significant temporal decline in $\delta^{15}N$ values in for uncorrected grilse ($n = 142$, $p < 0.001$), although this is skewed by high $\delta^{15}N$ values in 1985, and for mass-corrected grilse ($n = 94$, $p = 0.02$) Fig. 4.12a&b. This potentially indicates that grilse have been subject to a slight reduction in trophic level, and/or in baseline $\delta^{15}N$ conditions through the time period of this study. For the MSW fish, however (Fig. 4.12c&d), neither uncorrected nor mass corrected data showed any clear trends through time, suggesting that there have been no long term, directional changes in trophic level or in baseline $\delta^{15}N$ for

MSW salmon from this archive. These contrasting results for the cohorts are interesting, particularly as the lack of differences in values between the cohorts, both in δ^{13}C and in mass corrected δ^{15}N' values suggest that these fish are all feeding in similar areas. The differences in temporal trends in δ^{15}N values therefore imply changes in trophic level feeding in grilse that are not matched in the MSW fish. The lack of trend in the MSW mass corrected data suggests that there have been no directional changes in baseline δ^{15}N values. On this basis, the MSW fish may be better at selectively feeding at a consistent tropic level than the grilse in this population.

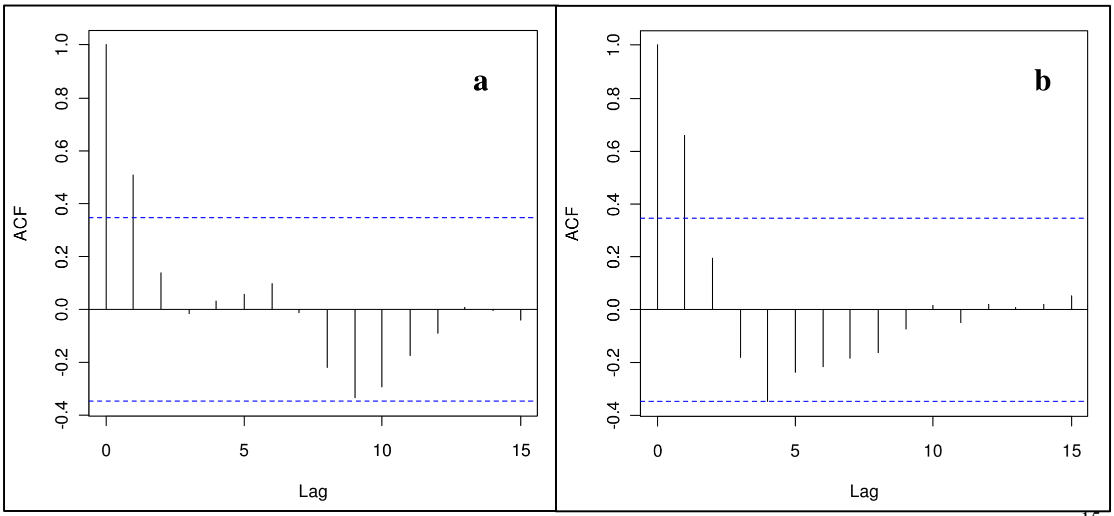


Figure 4.13. Correlograms showing autocorrelation (ACF) of the LOESS smoothed δ^{15}N value time series for a) Northeast Coast grilse and b) Northeast Coast MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

Fig. 4.13 shows strong autocorrelation in the time series of both grilse and MSW salmon from the Northeast Coast. In the grilse δ^{15}N data, there appears to be a return period of approximately six years, while this return period is much longer in the MSW δ^{15}N data at around 15 years, suggestive of a return period of around 10 years. The strong autocorrelations within these data, as with the River Frome, indicate strong non-random temporal control on the mechanisms controlling the δ^{15}N data. These mechanisms may include trophic level changes due to ecosystem structure, e.g. the dynamics of abundance in preferred prey species such as herring (Haugland et al. 2006; Holst et al. 1998; ICES 2009a; Jacobsen & Hansen 2001), or the basal ecosystem productivity dynamics (Hobson 1999; Jennings & Warr 2003; Lara et al. 2010; Rubenstein & Hobson 2004).

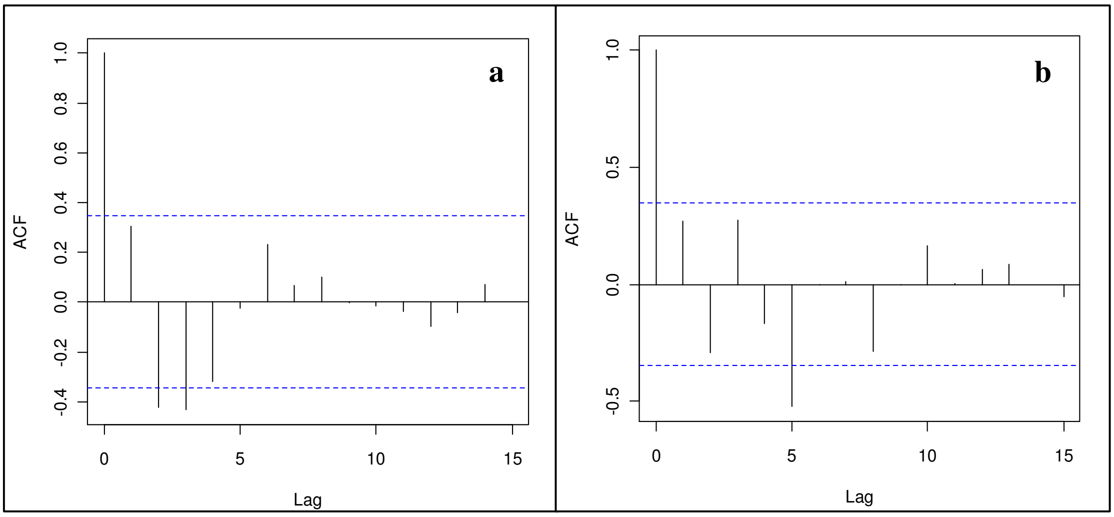


Figure 4.14. Correlograms showing autocorrelation (ACF) of the LOESS smoothed mass corrected $\delta^{15}N'$ value time series for a) Northeast Coast grilse and b) Northeast Coast MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

As Fig. 4.14 shows, the autocorrelation in the uncorrected $\delta^{15}N$ data from the Northeast Coast cohorts (Fig. 4.13) begins to break down post-mass correction, likely due to the missing years in the corrected data. The periodicity in the corrected grilse data is different to that seen in the uncorrected data above, with a negative correlation around two to three years, although the potential return period is the same at around six years, but this negative correlation becomes significant for grilse in these corrected data. The autocorrelation largely breaks down in the MSW data, however, although there is a significant, negative correlation at around five years. The observed change in MSW periodicity suggests that the major mechanisms controlling $\delta^{15}N$ and corrected $\delta^{15}N'$ values differ, although the increasing strength of the negative correlations in both cohorts after correction suggests that the process of correction may remove minor controlling signals, leaving the strongest underlying control apparent, likely either ecosystem baseline variation or variation in preferred prey abundance (Andreassen et al. 2001; Beaugrand et al. 2003; Cabana & Rasmussen 1996; Cherel et al. 2009; Peyronnet et al. 2008; Tamelander et al. 2009; Taylor et al. 1993). As suggested for the River Frome population, future work should be carried out to better identify causal mechanisms.

The ratio of measured (uncorrected) to expected (from the body mass and $\delta^{15}N$: mass relationship, as detailed in section 3.4) $\delta^{15}N$ values against time was plotted to further investigate the possibility of long-term trophic level reduction, see Fig. 4.15.

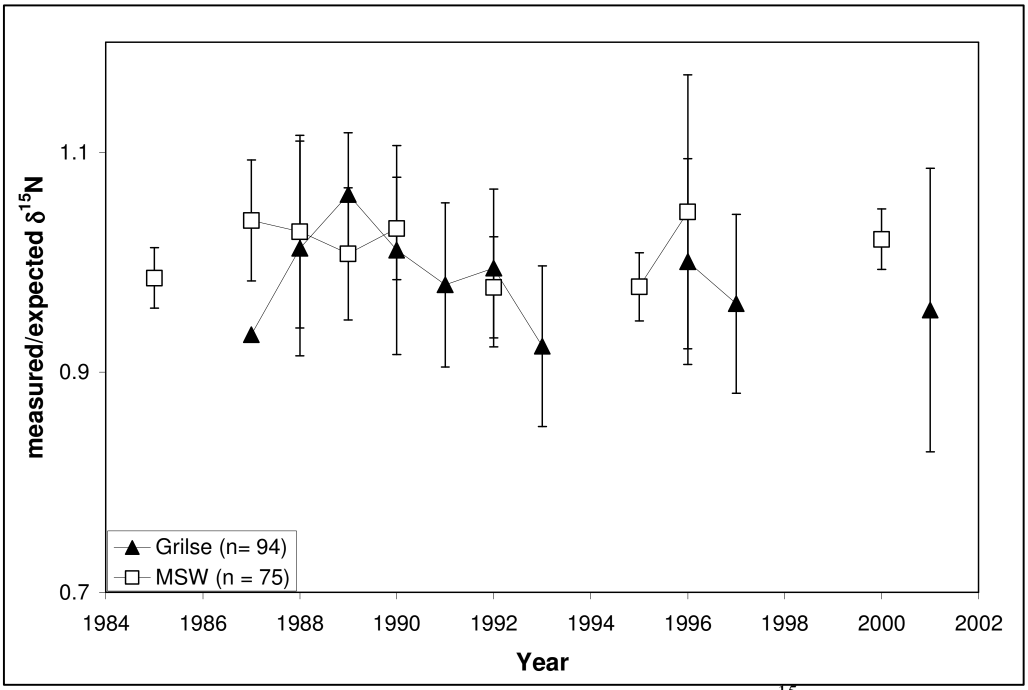


Figure 4.15. Ratio of mean measured: expected (based on mass) $\delta^{15}N$ values (‰) per year from the Northeast Coast for grilse (filled triangles) and MSW fish (empty squares) between 1971 and 2002; error bars are ±1SD, means used for graphical clarity.

A significant downward trend in trophic signal is seen in NEC grilse ($n = 94$, $p = 0.02$, see Fig. 4.15), indicating that the temporal decline in $\delta^{15}N$ values seen above in Fig. 4.12a&b is likely to be related to a trophic level decline. No significant decline in trophic signal is, however, seen in MSW salmon from the Northeast Coast over time, similarly to the River Frome cohorts. To test whether any temporal decline was apparent in the mass of the Northeast Coast fish analysed here, annual mass of each fish sampled for both cohorts was plotted against time, shown in Fig. 4.16.

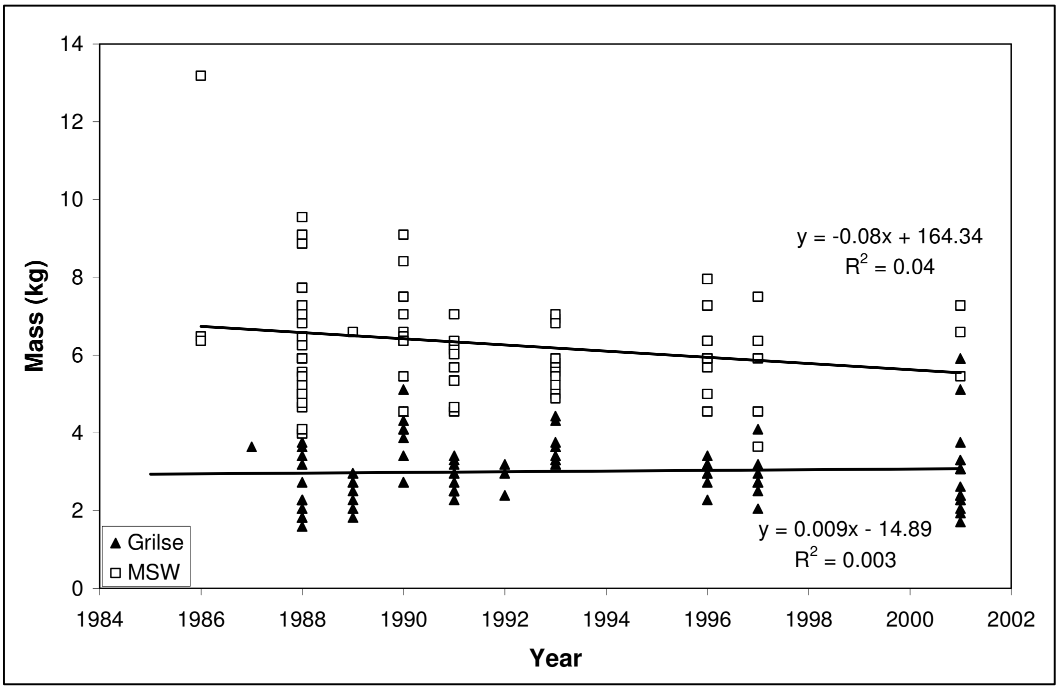


Figure 4.16. Mass (kg) per year from the Northeast Coast for salmon sampled between 1985 and 2001; grilse are shown as filled triangles and MSW fish as empty squares.

Despite an apparent trophic level reduction in Northeast Coast grilse seen above, there is no significant directional change in mass of either returning grilse or MSW salmon for the time covered by these analyses (see Fig. 4.16). These results are encouraging for this population, as they indicate that the relative potential fecundity per capita is not in decline, as may be the case for the River Frome grilse.

River Frome and Northeast Coast

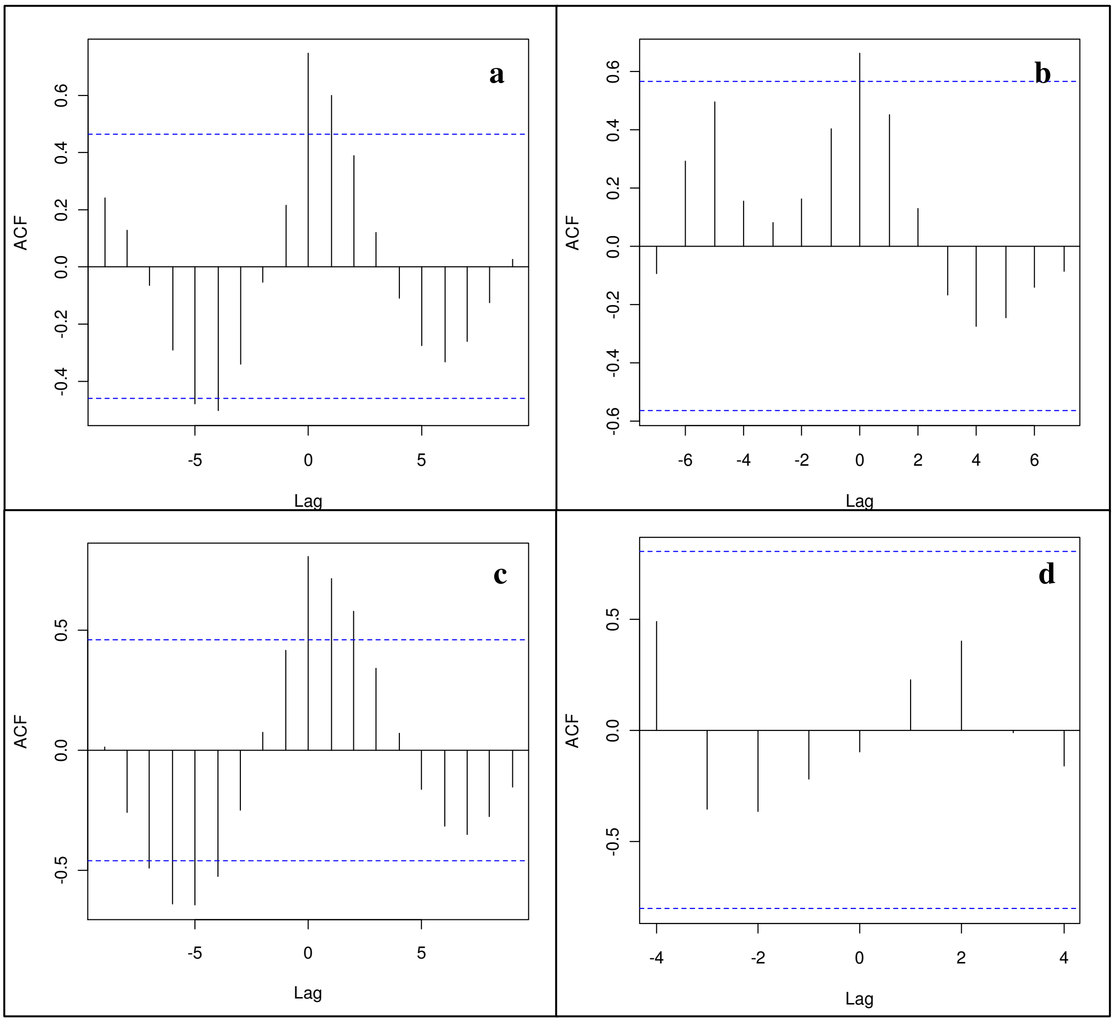


Figure 4.17. Correlograms showing cross-correlations (ACF) of the LOESS smoothed δ^{15}N value time series for a) RF grilse against RF MSW fish, b) NEC grilse against NEC MSW fish, c) mass corrected RF grilse against RF MSW fish and d) mass corrected NEC grilse against NEC MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The cross-correlation between uncorrected δ^{15}N data in the River Frome cohorts (Fig. 4.17a) shows that grilse and MSW fish from this population are positively cross-correlated at year zero, meaning that the patterns in each dataset are, as seen in the δ^{13}C data, immediately coincident. There are also negative cross-correlations around minus four to five and plus six years (non-significant), reflecting the autocorrelation structure in both time series. The immediate coincidence of δ^{15}N data, as with that seen in the δ^{13}C data, suggests that these cohorts are likely subject to similar climatic and/or prey conditions in the same year at sea. The mass corrected values show an almost identical pattern (Fig. 4.17c), but with stronger significance and one year extra on the negative lag in each direction. The Northeast Coast cohorts show similar positive cross-correlation between grilse and MSW fish at year zero (significant, see Fig. 4.17b), but the cross correlation structure is relatively weak, reflecting the weak autocorrelation structure in both time series. The patterns of cross-correlation lose all significance post-mass correction (Fig. 4.17d); the data are likely too sparse to draw any meaningful conclusions following removal of years with no mass values.

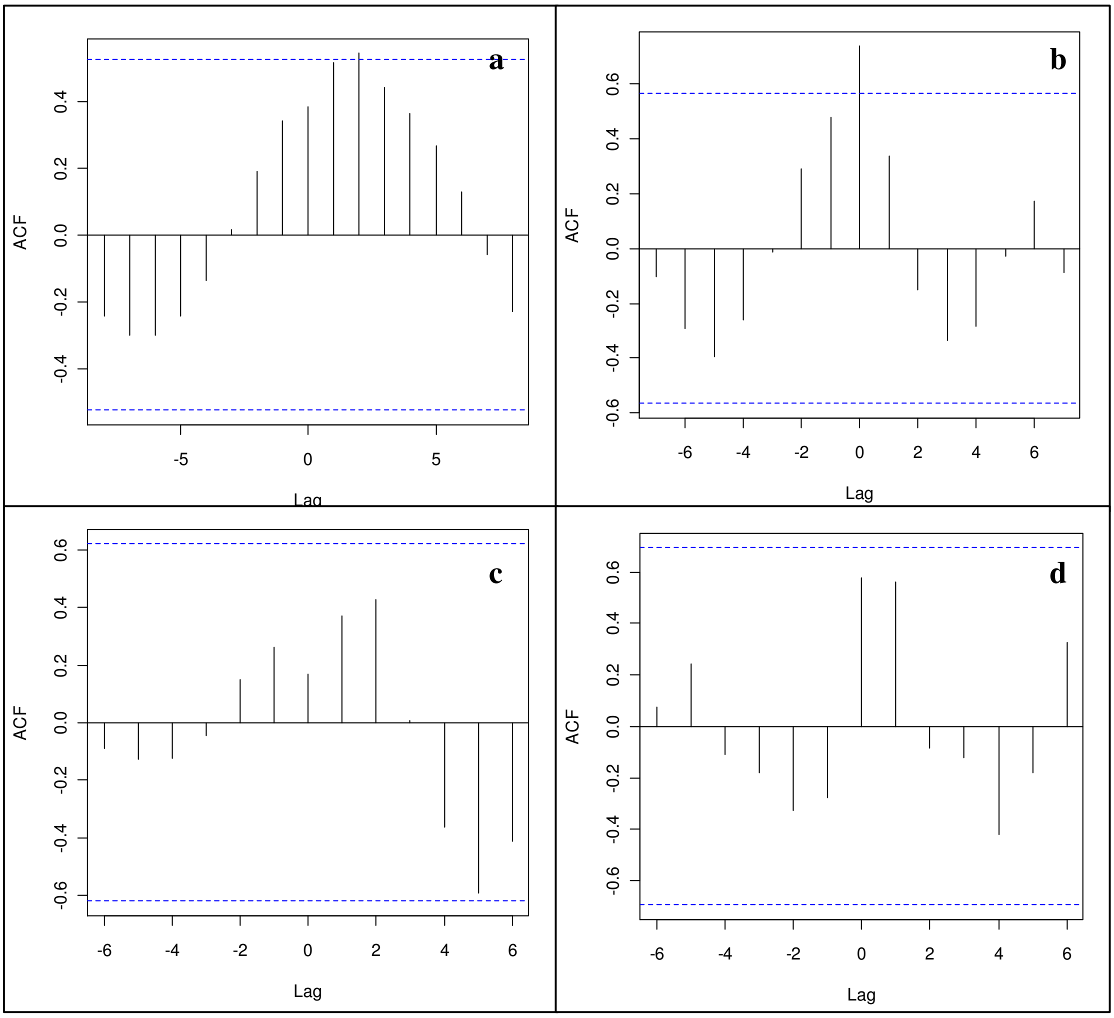


Figure 4.18. Correlograms showing cross-correlations (ACF) of the LOESS smoothed $\delta^{15}N$ value time series for a) RF grilse against NEC grilse, b) RF MSW fish against NEC MSW fish c) mass corrected RF grilse against mass corrected NEC grilse and d) mass corrected RF MSW fish against mass corrected NEC MSW fish. Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The cross-correlation of $\delta^{15}N$ values between River Frome and Northeast Coast grilse (Fig. 4.18a) shows a very strong structure with maximum positive correlations at a lag of two years (i.e. Northeast coast values preceding River Frome values by 2 years). The clear cross correlation implies that the dynamics controlling the $\delta^{15}N$ dynamics in both feeding grounds are linked. The mechanisms responsible are unclear, but may relate to prey species abundance dynamics, or baseline plankton dynamics. This observed structure largely breaks down after mass correction (Fig. 4.15c), likely due to the high number of missing years in the NEC grilse data. There is, again, strong cross-correlation between River Frome and Northeast Coast MSW fish (Fig. 4.18b), but with no lag; suggesting that prey species or baseline dynamics in $\delta^{15}N$ are temporally similar between the feeding grounds used by these MSW populations. This pattern, as with the grilse, weakens post-mass correction (Fig. 4.18d), which is also likely due to the missing years in the mass corrected Northeast Coast data. The disparate relationships between $\delta^{15}N$ values are difficult to explain, hinting either at co-incidental cross correlation structure, or complex, basin-wide ecosystem-climate dynamics.

4.3. $\delta^{13}C$ and $\delta^{15}N$ data

Having assessed within and between population trends in $\delta^{13}C$ and $\delta^{15}N$ values individually, these isotope trends were then compared to determine whether any temporal relationships between the $\delta^{13}C$ and $\delta^{15}N$ compositions of the sampled fish could shed light on controlling mechanisms of isotopic variation. In the River Frome grilse (Fig. 4.19a), carbon and nitrogen values show significant positive correlations with a positive lag of four to six years between the $\delta^{13}C$ and $\delta^{15}N$ values, and negative correlations with a negative lag of minus two years. $\delta^{15}N$ values thus trail $\delta^{13}C$ values by around 5 years. The positive pattern is similar in the mass corrected grilse (Fig. 4.19c), but with no significant lag previous to year zero. The MSW fish show a similar pattern (Fig. 4.19b), with positive correlations with a 5 year lag. MSW data show oscillating cross correlation structure with an apparent return period of around 14-15 years, but confidence in this figure is limited by the relatively short duration of the time series. The pattern is made stronger by mass correction (Fig. 4.19d), indicating that size effects are not controlling factors in these cross-correlations.

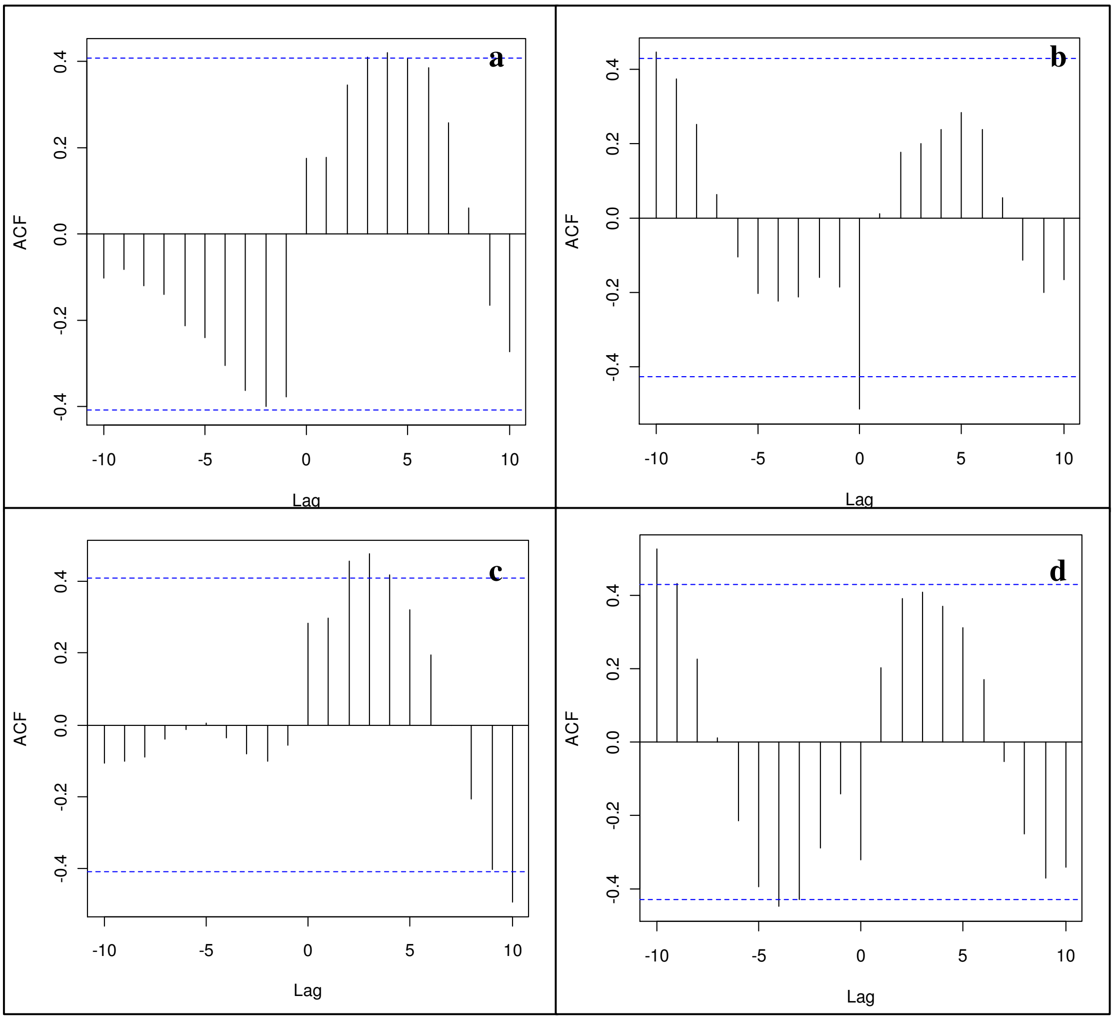


Figure 4.19. Correlograms showing cross-correlations (ACF) between LOESS smoothed $\delta^{13}C$ and $\delta^{15}N$ value time series for a) RF grilse (uncorrected $\delta^{15}N$), b) RF MSW fish (uncorrected $\delta^{15}N$), c) RF grilse (mass corrected $\delta^{15}N'$), and d) RF MSW fish (mass corrected $\delta^{15}N'$). Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The Northeast Coast grilse (Fig. 4.20a) data show no significant correlations between $\delta^{13}C$ and $\delta^{15}N$ values in the uncorrected data, although there is structure inherent within the cross-correlation patterns. Similarly to the River Frome data, there is a suggestion of cross correlation with a lag of 4-5 years, and negative correlation with zero lag. There is, however, a significant, positive correlation at minus one year for the mass-corrected data (Fig. 4.20c), indicating highest $\delta^{15}N$ values in the year following highest $\delta^{13}C$ values. In the MSW fish uncorrected data (Fig. 4.20b), the pattern is very similar to that seen in the uncorrected grilse, but stronger with a significant positive lag of minus three to four years between the $\delta^{13}C$ and $\delta^{15}N$ values. The pattern again appears to break down in the mass corrected MSW data (Fig. 4.20d), with non-significant and sparse correlations.

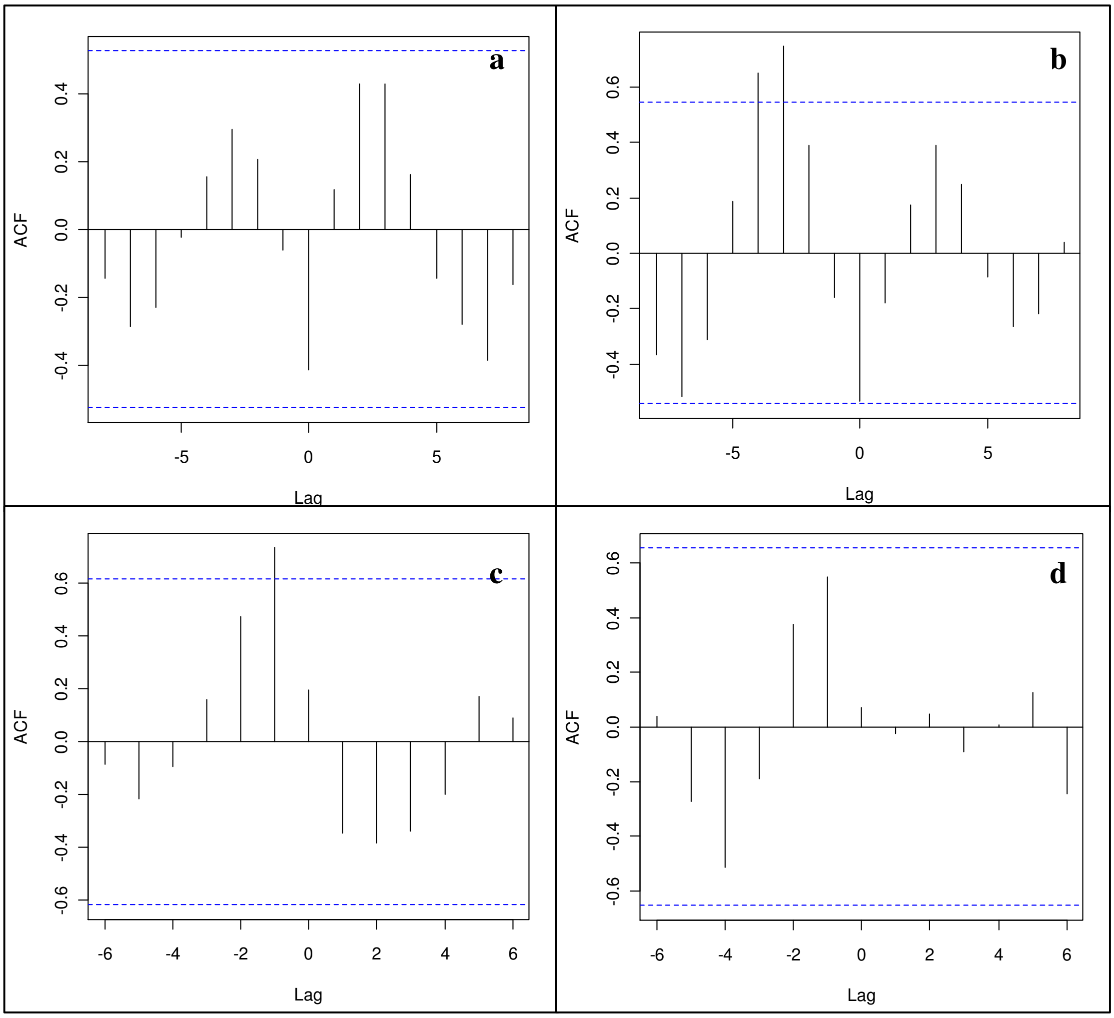


Figure 4.20. Correlograms showing cross-correlations (ACF) between LOESS smoothed $\delta^{13}C$ and $\delta^{15}N$ value time series for a) NEC grilse (uncorrected $\delta^{15}N$), b) NEC MSW fish (uncorrected $\delta^{15}N$), c) NEC grilse (mass corrected $\delta^{15}N'$), and d) NEC MSW fish (mass corrected $\delta^{15}N'$). Lag is in years, dashed lines show significance at $\alpha = 0.05$.

The apparent patterns in Figs 4.19 and 4.20 strongly suggest time-lagged linkages between the conditions controlling $\delta^{13}C$ values and those controlling $\delta^{15}N$ values in the tissues of Atlantic salmon. It seems likely that climatic factors such as temperature have a rapid effect on phytoplankton growth rates (and therefore baseline $\delta^{13}C$ values in the same year). The subsequent effects of high or low plankton growth will cascade through food webs to influence the abundance of higher trophic level prey over a range of timescales. It appears that the temporal delay between changes in plankton growth conditions and availability or composition of prey items in salmon averages around 3-5 years, possibly reflecting the spawning and recruitment dynamics of preferred prey items under differing environmental conditions (Beare et al. 2004a; Beare et al. 2004b; Friedland et al. 2000; Holst et al. 1998; ICES 2009a; Kallio-Nyberg et al. 1999; Stenseth et al. 2002). These hypotheses may be investigated further by integrating isotopic data with extensive CPR and fishery databases.

4.4. Returns

Data on numbers of adult salmon returning to the River Frome have been collected since the installation of a fish counter, which has been recording upstream movements of returning adult salmon since 1973 at the Salmon & Trout Research Centre, East Stoke, Dorset. This facility is owned by the Institute of Freshwater Ecology and currently operated by the Game and Wildlife Conservation Trust (GWCT, 2008 onwards); it was previously operated by the Centre for Ecology and Hydrology (CEH, 1965 – 2008), funded by the Natural Environment Research Council (NERC). Counts of fish are recorded by a Scottish Hydro-Electric (formerly North of Scotland Hydro-electric Board (NSHEB)) Mk Xb resistivity counter. The counter is connected to three stainless steel electrodes mounted 450 mm apart on the Environment Agency venturi gauging weir at East Stoke on the River Frome in Dorset. Adult salmon count data are verified by a combination of trace waveform analysis (Beaumont et al. 1986), video frame-grab and videotape analysis (Beaumont et al. 2009). The returns data used here, as shown in Fig. 4.21, were kindly provided by W.R.C. Beaumont and A.T. Ibbotson during operation of the facility by CEH, and are the net count data, after counts of salmon dropping back after ascending through the counter have been removed from the gross count figures.

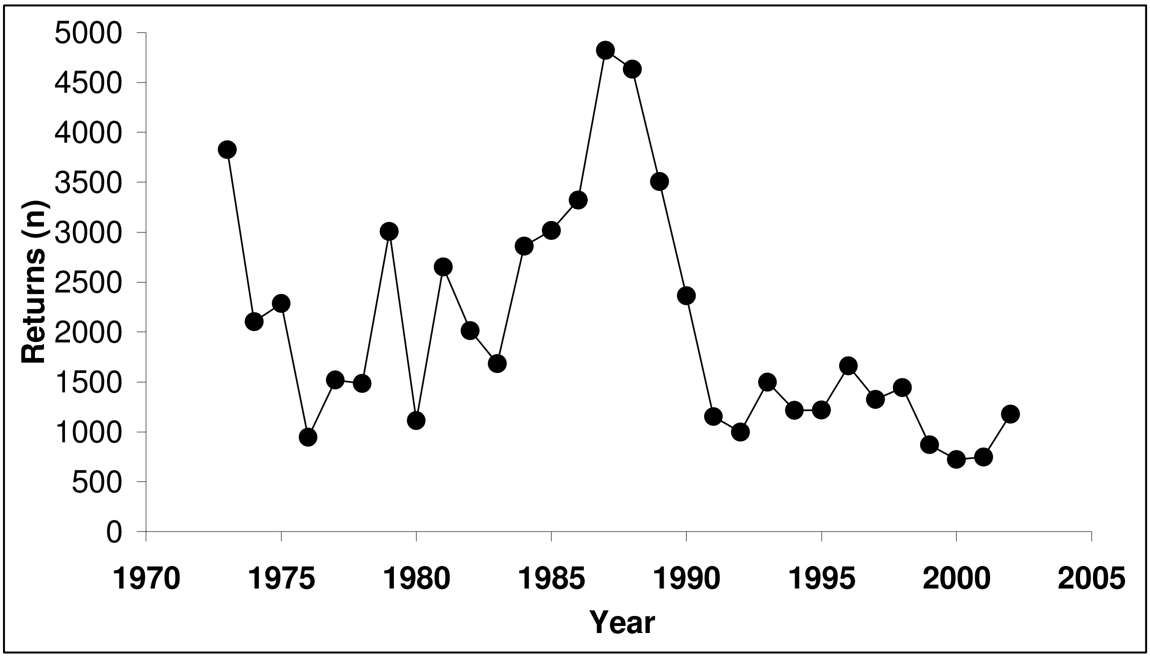


Figure 4.21. Net counts of returning adult salmon passing the East Stoke fish counter per year, 1973-2002 (CEH, unpubl. data).

The numbers of salmon returning to the River Frome, as shown above in Fig. 4.21, initially fluctuated from the installation of the counter in 1973 onward throughout the 1970s, with a high of 3,827 in 1973 and a low of 945 in 1976. During the 1980s returning fish rose sharply to their highest number with a peak of 4,822 in 1987, before declining to less variable but much lower numbers in the 1990s to the early 2000s, reaching an overall low of only 722 returning adults in 2000. Unfortunately, numbers of out-migrating smolts against which to normalise these data are not currently available.

Returns data to the Northeast Coast driftnet fishery, however, are not available as the catch statistics do not represent abundance. The fishery is being progressively phased out; consequently there has been a substantial decline in the effort and increase in other restrictions, which have led to variations in catches that are unreflective of variations in abundance. Equally, an unknown and variable proportion of salmon within the Northeast Coast fishery originate from Scottish rivers, thus any returning stock estimates for individual English or Scottish rivers may not reflect abundance of fish represented by the Northeast Coast driftnet archive. The best estimate of fish abundance, based on advice from Mark Ives at Cefas (pers. comm.), is the pre-fishery abundance (PFA) annual figures for England and Wales, published annually by ICES; unfortunately, as with the Frome data it is not currently possible to normalise the PFA figures to smolt numbers. Salmon from the River Tyne, which is one of the most productive rivers for salmon in Britain (Mawle & Milner 2003), are likely to make up a large component of both fish represented in the model and fish returning to the Northeast Coast, where they were caught in the driftnet fishery.

The abundance estimates of salmon returning to the Northeast Coast, as represented by the ICES PFA model estimates shown below in Fig. 4.22 (ICES 2008a), show an overall pattern of decline in both grilse and MSW fish. Within these declines, there appear to be multi-year oscillations on an approximately 6 to 8 year basis, similar, although differing in relative magnitude, to those shown in the δ^{13}C values of both cohorts through time.

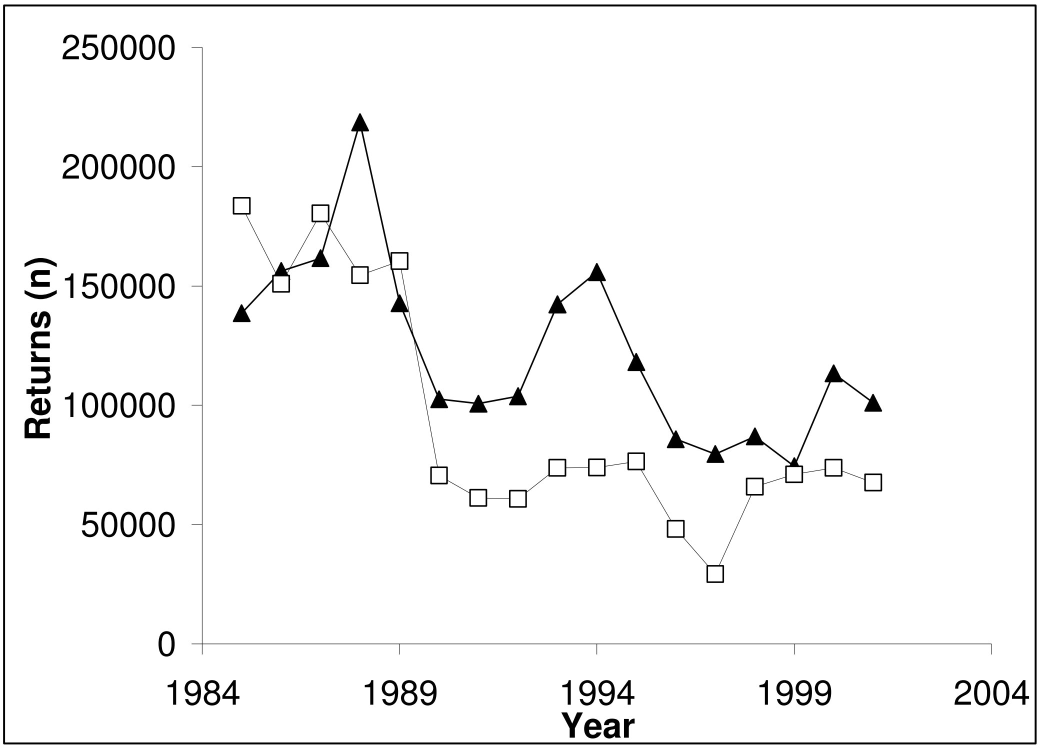


Figure 4.22. Annual ICES PFA estimates for England and Wales for grilse (filled triangles) and MSW fish (empty squares) between1984-2001 (ICES 2008a).

The numbers of salmon returning to the River Frome are strongly, significantly cross-correlated at year zero with the ICES PFA models for both grilse (Fig. 4.23a) and MSW fish (Fig. 4.23b), which are also strongly, significantly cross-correlated with one another (Fig. 4.23c). These correlations show that salmon returning to both UK populations studied here are subject to similar patterns of returns throughout the time in which they are coincident (1985 to 2001), which indicates that these fish may have been subject to similar overall controls on their returns since the mid-1980s. In order to investigate the controls on returns further, the annual numbers of fish returning to the River Frome and in the ICES PFA models for grilse and MSW fish were cross-correlated with stable isotope time series for each population and cohort.

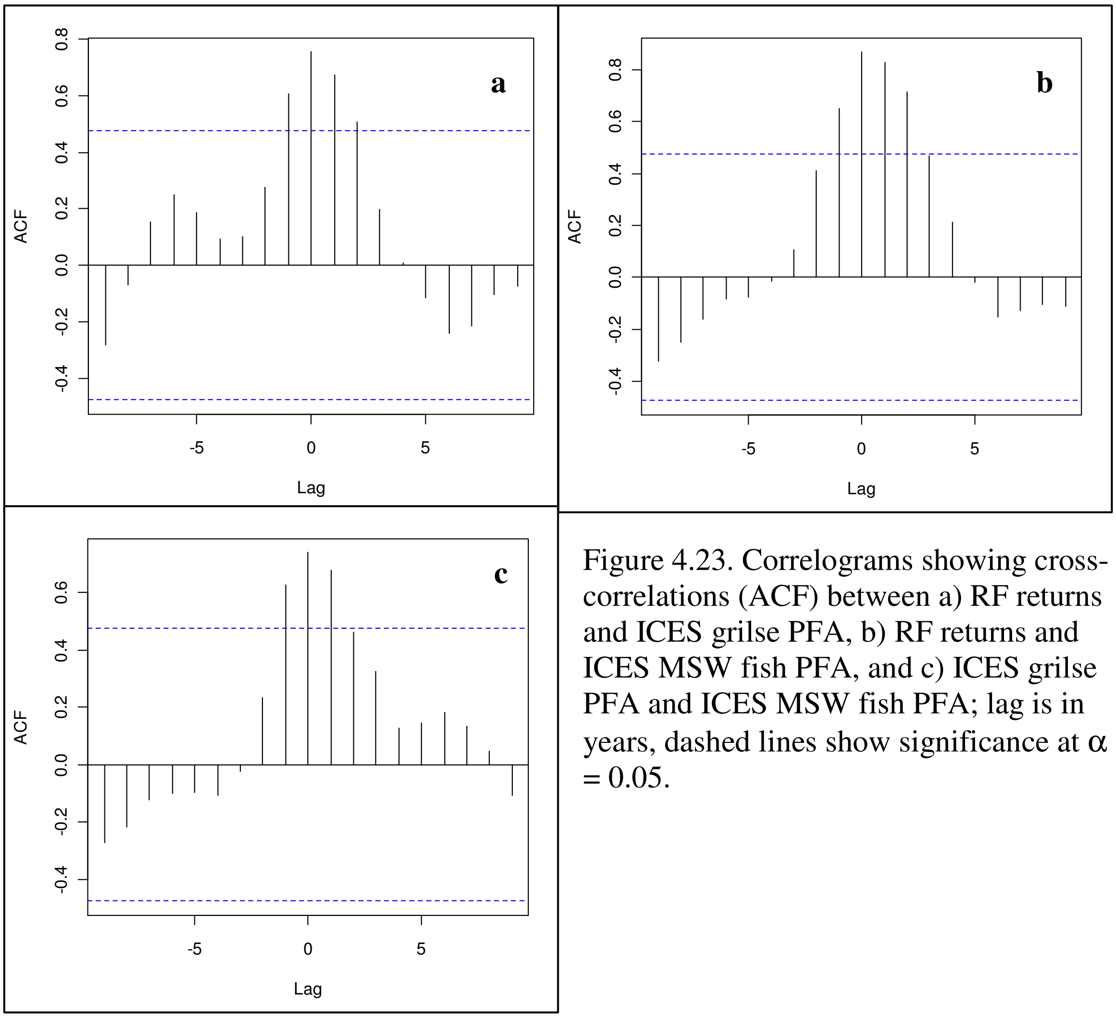


Figure 4.23. Correlograms showing cross-correlations (ACF) between a) RF returns and ICES grilse PFA, b) RF returns and ICES MSW fish PFA, and c) ICES grilse PFA and ICES MSW fish PFA; lag is in years, dashed lines show significance at α = 0.05.

4.5. Relationships between returns, $\delta^{13}C$ & $\delta^{15}N$ values and NAO

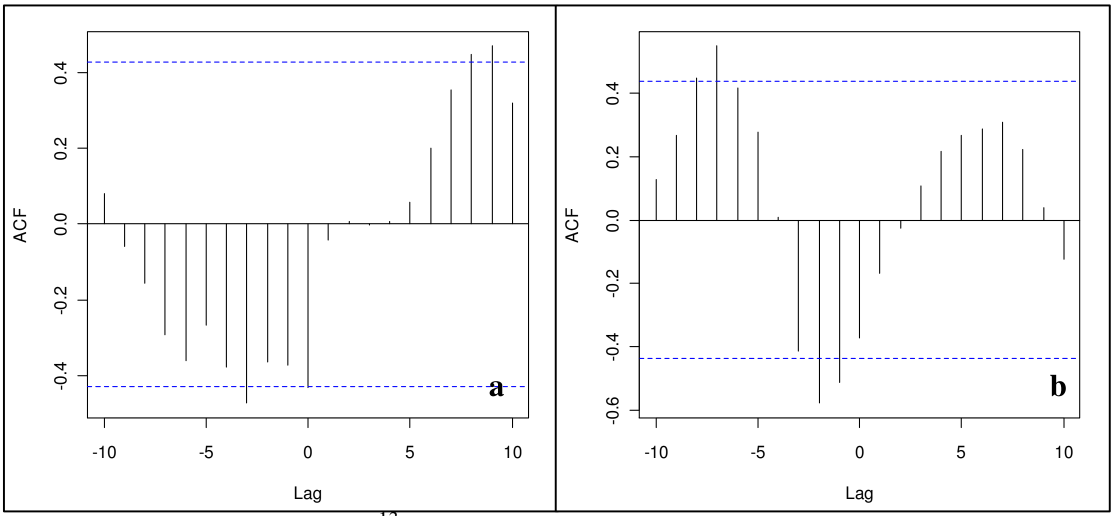


Figure 4.24. Correlograms of $\delta^{13}C$ values (‰) against returning fish count data (per year) from the River Frome for a) grilse and b) MSW fish; lag is in years, dashed lines show significance at $\alpha = 0.05$.

The River Frome archive shows a significant negative cross-correlation between $\delta^{13}C$ values and returning fish numbers with lags between zero and minus three years (i.e. conditions producing negative $\delta^{13}C$ values are likely to result in higher returns for a period of up to three years) Fig. 4.24. There is a clear oscillating pattern, with a return period of approximately 14 years in MSW fish. As has previously been discussed (see section 3.3, above), $\delta^{13}C$ values in marine foodwebs are most likely intrinsically linked to temperature (Barnes et al. 2009; Hofmann et al. 2000; Lara et al. 2010). Many areas within the marine life history of the Atlantic salmon have been shown to be strongly influenced by SST, including growth rate, both somatic and gonadal, lipid versus protein storage, availability of prey items, and metabolic rates (Anderson 1997; Beaugrand & Reid 2003; Friedland 1998; Friedland et al. 2005; Friedland et al. 1999; Friedland et al. 2000; Friedland et al. 2009; Friedland & Reddin 2000; Hansen et al. 2003; Hughes & Turrell 2003; Jonsson & Jonsson 2004a; Jonsson & Jonsson 2004b; Marschall et al. 1998; Peyronnet et al. 2008; Peyronnet et al. 2007; Reddin & Friedland 1993; Todd et al. 2008). Variation in these factors is thought to play a key role in controlling salmon survival and return rates. If temperature variations were exercising a strong control on numbers of salmon surviving to return to their natal streams, some level of correlation between $\delta^{13}C$ values and numbers of returning fish would be expected. This suggests that, for the River Frome archive, correlation between variations in ocean climatic conditions experienced by the salmon at sea and numbers of returning salmon, either as grilse or as MSW fish is offset by several years. The proximity to zero years of the significant, negative cross-correlations suggest that returns to the Frome are lower around years of higher SST values. Given the importance of variability in SST found by many studies, two things may be concluded from this:

1. Ocean climate variability (as represented by variability in $\delta^{13}C$ values) in feeding grounds for Frome salmon is probably quite low given the relatively small variation in $\delta^{13}C$ values (this is discussed further in the temporal analyses of $\delta^{13}C$ values, see also Table 3.7, above) and likely has cyclic patterns over decadal plus timescales;

and

2. The zero year (grilse) and minus one to two year (MSW) negative cross-correlations suggest that returns are high when $\delta^{13}C$ values are low, likely as a result of lower oceanic temperatures. Ocean climate variability and physiological parameters intrinsically linked to it appear to be exerting control on levels of mortality and return rates of Atlantic salmon to the River Frome.

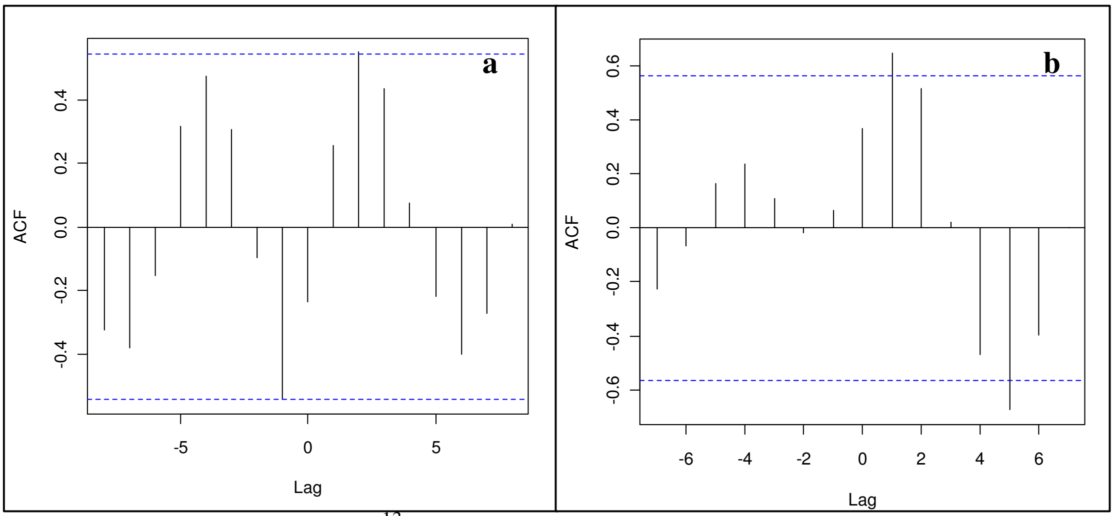


Figure 4.25. Correlograms of $\delta^{13}C$ values (‰) against returning fish count data (per year) from the ICES PFA model (ICES 2008a) for a) NEC grilse and b) NEC MSW fish; lag is in years, dashed lines show significance at $\alpha = 0.05$.

The Northeast Coast archive shows a significant, negative relationship between $\delta^{13}C$ values and ICES PFA numbers for grilse at minus one year, very similar to that seen in the River Frome fish, and a strong oscillating correlation structure with a return period of around 6 years (Fig. 4.25a). The correlation structure is much weaker for MSW fish (Fig. 4.25b), with positive correlation with a lag of 1 year and negative correlation at a lag of plus five years. These results suggest that the numbers of grilse returns are influenced by the conditions controlling $\delta^{13}C$ values the previous year, although this pattern is not clear in MSW fish. Ocean climate variability is considerably higher in the feeding grounds used by the Northeast Coast population than on the River Frome population's feeding grounds (see Table 3.7), which logically indicates that this variation would be expected to have a stronger effect on returns to the Northeast Coast than to the River Frome. Given the importance of variability in SST found by many studies, two things may be concluded from this:

1. Ocean climate variability (as represented by variability in $\delta^{13}C$ values) in feeding grounds for Northeast Coast salmon is probably quite high given the large variation in $\delta^{13}C$ values (this is discussed further in the temporal analyses of $\delta^{13}C$ values, above);

and

2. Ocean climate variability and physiological parameters intrinsically linked to it are likely to be controlling levels of mortality and return rates of Atlantic salmon (especially grilse) to the Northeast Coast.

The return period of four to six years within the Northeast Coast grilse cross-correlations is also shorter than in the Frome, which shows a minimum return period of approximately 15 years. This implies that both the amplitude and frequency of climate variations are higher in the Northeast Coast feeding grounds.

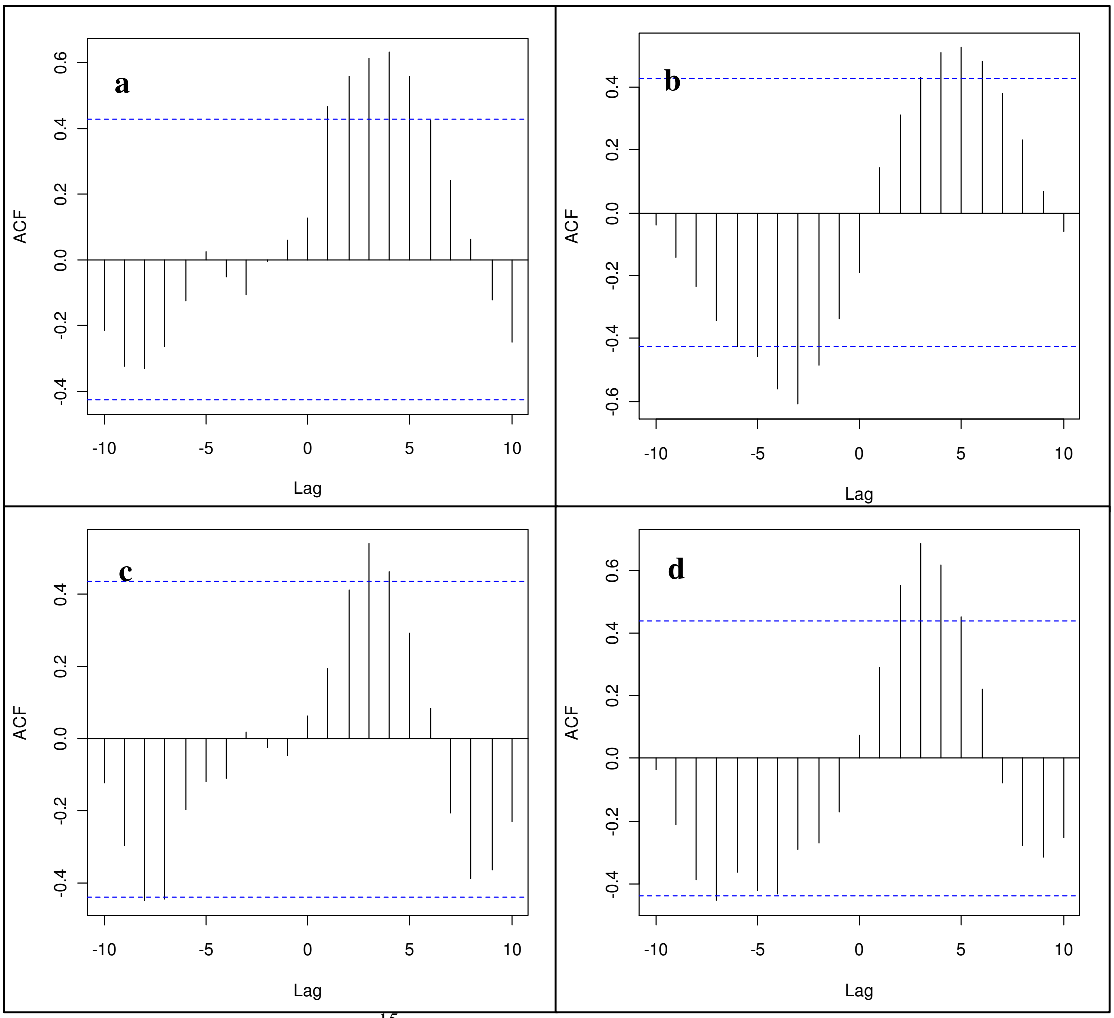


Figure 4.26. Correlograms of $\delta^{15}N$ values (‰) against returning fish count data (per year) from the River Frome for a) grilse, b) mass corrected grilse, c) MSW fish and d) mass corrected MSW fish; lag is in years, dashed lines show significance at $\alpha = 0.05$.

Salmon from the River Frome archive show lagged significant relationships between returns and uncorrected $\delta^{15}N$ values for both grilse and MSW fish, see Fig. 4.26a&c, Both cohorts show significant, positive relationships between returns and $\delta^{15}N$ values, uncorrected and mass corrected, with a lag of plus three years in MSW fish and plus five years in grilse, and negative relationships with a lag of minus 8 years in both cohorts. It is difficult to explain these results other than to invoke somewhat vague dynamics of prey abundance, and it is also possible that the strong cyclic autocorrelation in the $\delta^{15}N$ values drives the observed patterns. The patterns for both grilse and MSW salmon remain very similar after correction for mass (see Fig. 4.26b&d), but with the most significant, positive relationship at a lag of plus four years for the grilse, and the significant negative lags coming earlier for both cohorts at minus four to seven years. As discussed above, trophic level is a large component in defining $\delta^{15}N$ values, but there is little evidence for a relationship between marine mortality and trophic level given the very small post-mass correction changes. Assuming that mass correction removes the majority of within-cohort trophic level effects, as discussed above, the remaining signal is largely that of baseline or prey abundance variation reflected in the $\delta^{15}N$ composition incorporated by the fish in their feeding grounds. When comparing the effects of trophic level and mass correction, it appears that the majority of the variation in $\delta^{15}N$ is controlled by baseline variation, with an additional amount controlled trophically. Interestingly, there is significantly more variation in $\delta^{15}N$ values during years with lower numbers of returns (<2500) than higher (≥ 2500) in uncorrected grilse (F test <2500, >2500: $n = 15,7$, $df = 14$, $F = 6.20$, $p = 0.02$), which implies that fish are feeding across a broader range of trophic levels, and less selectively in less favourable years at sea, potentially resulting in fewer returning grilse.

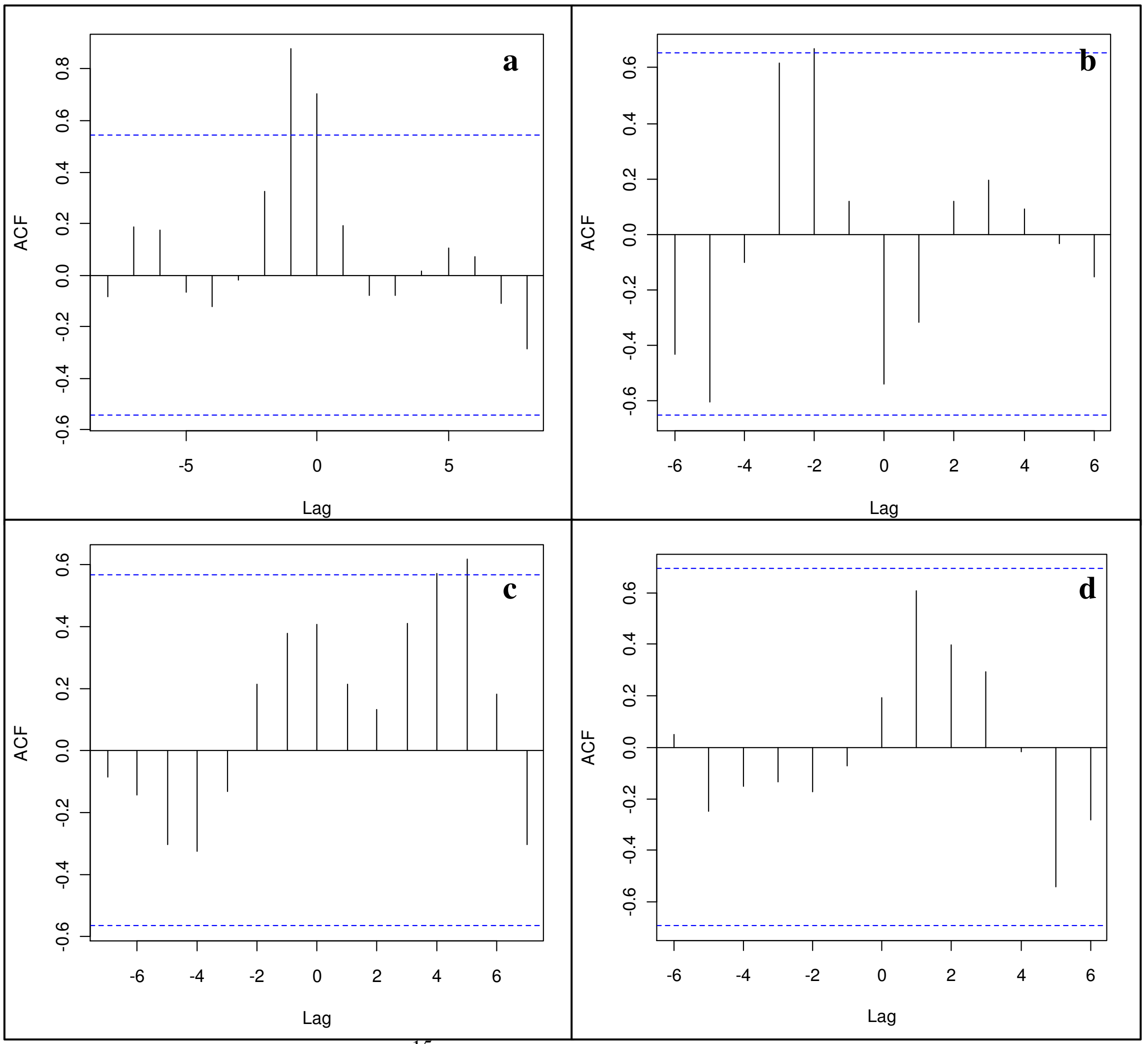


Figure 4.27. Correlograms of δ^{15}N values (‰) against ICES PFA model numbers (per year) from the Northeast Coast for a) grilse, b) mass corrected grilse, c) MSW fish and d) mass corrected MSW fish; lag is in years, dashed lines show significance at $\alpha = 0.05$.

Northeast Coast grilse show a significant, positive relationship between returns and uncorrected δ^{15}N values with lags of zero and minus one (Fig. 4.27a). As this relationship weakens post-mass correction (Fig. 4.27b), it is possible that there is a trophic level control on grilse from this population, however the low sample numbers after mass correction may also influence this result. In the MSW fish there is a significant, negative correlation with no lag, and, similar to the grilse, a positive cross-correlation at a lag of minus two years (Fig. 4.27c). There is, however, no significant post-mass correction relationship between δ^{15}N values and returns in Northeast Coast MSW salmon (Fig. 4.25d). It appears from these cross-correlations that trophic level varies with returns in salmon from the Northeast Coast population as the significance levels reduce after the removal of mass effects, but there is little evidence for a relationship between marine mortality and trophic level given the very small post-mass correction changes. There is also evidence for controls on mortality stemming from variation in preferred prey abundance or from environmental factors controlling $\delta^{15}N$ values, as there are still positive cross-correlation patterns in the mass corrected data for both cohorts.

The above analyses of $\delta^{15}N$ against returns are interesting from the perspective of linking trophic ecology and oceanic conditions to population dynamics in the salmon populations analysed here. Favourable years for returns appear to potentially be linked to the dynamics of high trophic level prey items, prey species abundance and ecosystem baseline ^{15}N dynamics, but the nature of these relationships are highly varied between populations and cohorts. The variable lags and sign of correlations between returns and $\delta^{15}N$ values may suggest that any relationships are circumstantial, reflecting other linked variables, rather than direct. Linkages may be mediated through the salmon feeding more selectively, and selecting larger, higher reward prey, during favourable oceanic conditions for either general food availability, or through the availability of the preferred prey types after changes in baseline plankton conditions. The wider variability in $\delta^{15}N$ values in years of low returns to the Frome, together with the likely correlation between Northeast Coast MSW salmon trophic level and returns in the ICES PFA model data are strongly suggestive of a link between adult survivorship to successful return and the availability at sea of higher trophic level prey for grilse and greater levels of baseline productivity for MSW fish. In the North Atlantic, productivity is positively correlated with baseline $\delta^{15}N$ values (Waser et al. 2000), indicating that there will be more food resources available in ecosystems with higher baseline $\delta^{15}N$ values. Variation in salmon $\delta^{15}N$ values, therefore, is likely to reflect a combination of trophic level and basal ecosystem effects (Mendes et al. 2007). Similar links between higher trophic level prey, greater oceanic productivity and increased marine survival have previously been found in Pacific salmon (Beamish et al. 1997; Daly et al. 2009). These findings have important ramifications for the management of both populations analysed here, where it would be interesting to determine, perhaps based on the Continuous Plankton Recorder and ocean colour observations, whether there are, as the cross-correlations in Figs 4.24, 4.25, 4.26 and 4.27 suggest, taxonomic and productivity differences between plankton in years with good versus bad numbers of returning fish, thereby building a mechanism for prediction of returns through observation of plankton and productivity changes.

It might be assumed that relationships between numbers of returning salmon and $\delta^{15}N$ values would be echoed in similar relationships between mass and returns. To test whether the correlations between salmon $\delta^{15}N$ values and returning numbers of adult fish were reflected in mass, and also whether the temporal decline in the size of grilse, see section 4.2, was influencing returning population size, annual mean mass for each cohort was plotted against returns, see Fig. 4.28.

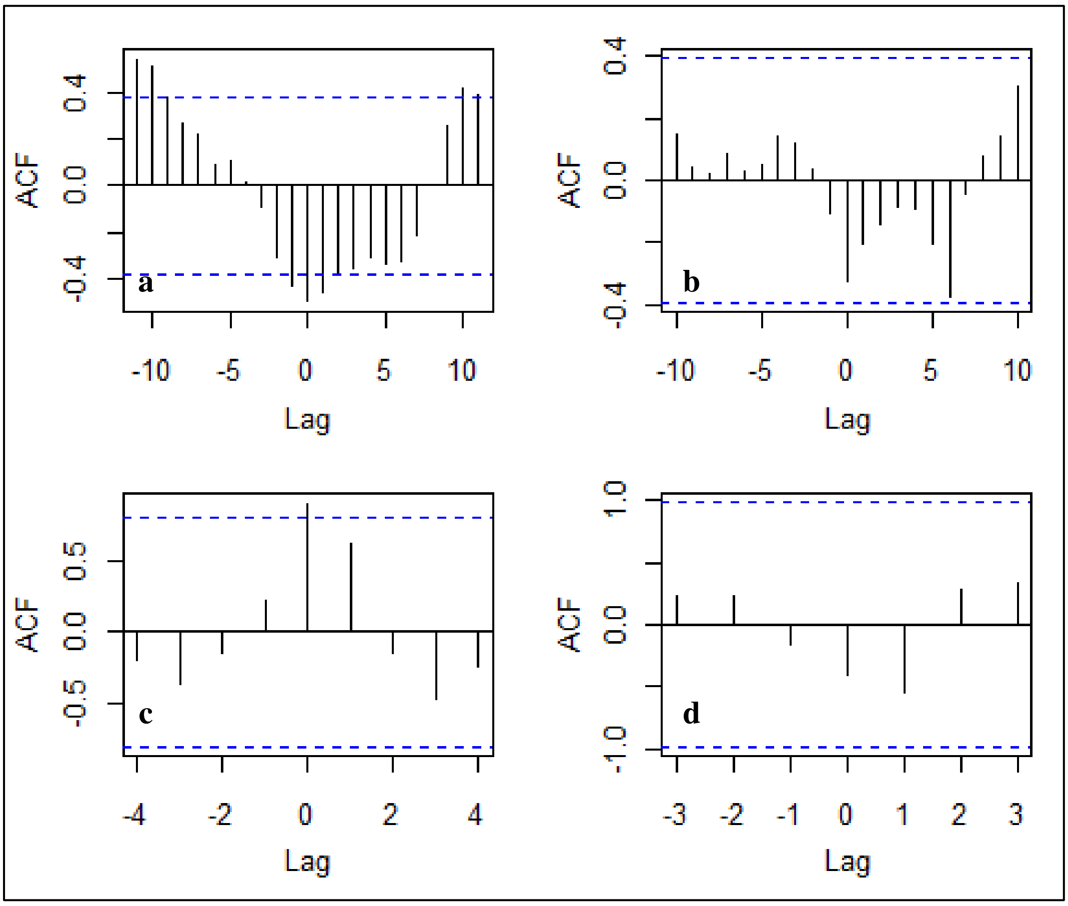


Figure 4.28. Correlograms of mean mass (kg) per year for a) RF grilse against returns, b) RF MSW fish against returns, c) NEC grilse against ICES PFA grilse and d) NEC MSW fish against ICES PFA MSW; lag is years, dashed lines are significant at $\alpha = 0.05$

Surprisingly, a significant negative relationship was seen between mass and returning numbers of adult salmon in River Frome grilse (Fig. 4.28a), and the suggestion of a similar relationship in MSW fish (4.28b). This may be due to the minimal numbers of fish in each cohort for which mass values are available ($n < 200$) being used to represent the entire mass range of this population. In Northeast Coast grilse, however, there is a significant, positive relationship between mass and ICES PFA grilse model numbers (Fig. 4.28c), as might be expected if larger fish were more likely to survive and return (Andreassen et al. 2001; Jonsson & Jonsson 2004a;

Peyronnet et al. 2007). No clear relationship could be seen between mass and ICES PFA MSW model numbers for Northeast Coast MSW salmon (Fig. 4.28d). These results mean that, with the exception of Northeast Coast grilse, the positive relationship between δ^{15}N values and returns is not echoed by mass, as might be expected from a trophic signal, which corresponds with the finding that the correlations between nitrogen isotope values and returns are higher for the δ^{15}N' values in the River Frome (Fig. 4.26). If the signal is largely not trophic, this result adds weight to the theory that higher marine productivity associated with higher baseline δ^{15}N values is more favourable to survival to river return. While size at return may be declining over time for River Frome grilse and Northeast Coast MSW fish, this mass reduction does not appear to be negatively affecting the overall numbers of these returning fish. Possibly density-dependent in-stream processes limit the carrying capacity of their home rivers, as observed in other Atlantic salmon rivers (Cunjak & Therrien 1998), where availability of suitable juvenile habitat defines the quantity of emigrating smolts. This would mean that any changes in the relative fecundity of spawning adults have not greatly affected the smolt production of this river. It would be useful to investigate emigrating numbers of smolts to determine whether this is the case in either population.

Various studies have found links between abundance of Atlantic salmon and the winter North Atlantic Oscillation Index (wNAOI) (e.g. Jonsson & Jonsson 2004b; Peyronnet et al. 2008). To test whether this climate index plays a role in controlling returns of salmon to the River Frome or in the ICES PFA grilse and MSW fish models, cross correlations were run between the NAO and these data (see Fig. 4.29).

The significant, positive correlation between the River Frome returns and wNAOI at a lag of minus two years (Fig. 4.29a) indicates that returns are highest to the River Frome two years before wNAOI is at its highest, which shows an unusual link between positive NAOI and higher salmon survival. This cross-correlation likely has a return period greater than 20 years, meaning that the timescale of these analyses may not be sufficient to elucidate genuine relationships in the data. There is no significant relationship observed between the ICES PFA grilse model and wNAOI (Fig. 4.29b), but there is a significant, positive relationship between wNAOI and the ICES PFA MSW fish model (Fig. 4.29c), with a lag of minus four to five years, and a return period beyond the temporal coverage of these analyses. The observed relationship in Fig. 4.29c suggests that the ICES PFA MSW fish model has highest predicted returns four to five years after the highest wNAOI values, possibly in conditions of cooler winters and warmer summers. Future work should investigate these returns linkages more thoroughly, using further UK stocks to elucidate the mechanisms behind such climate index relationships.

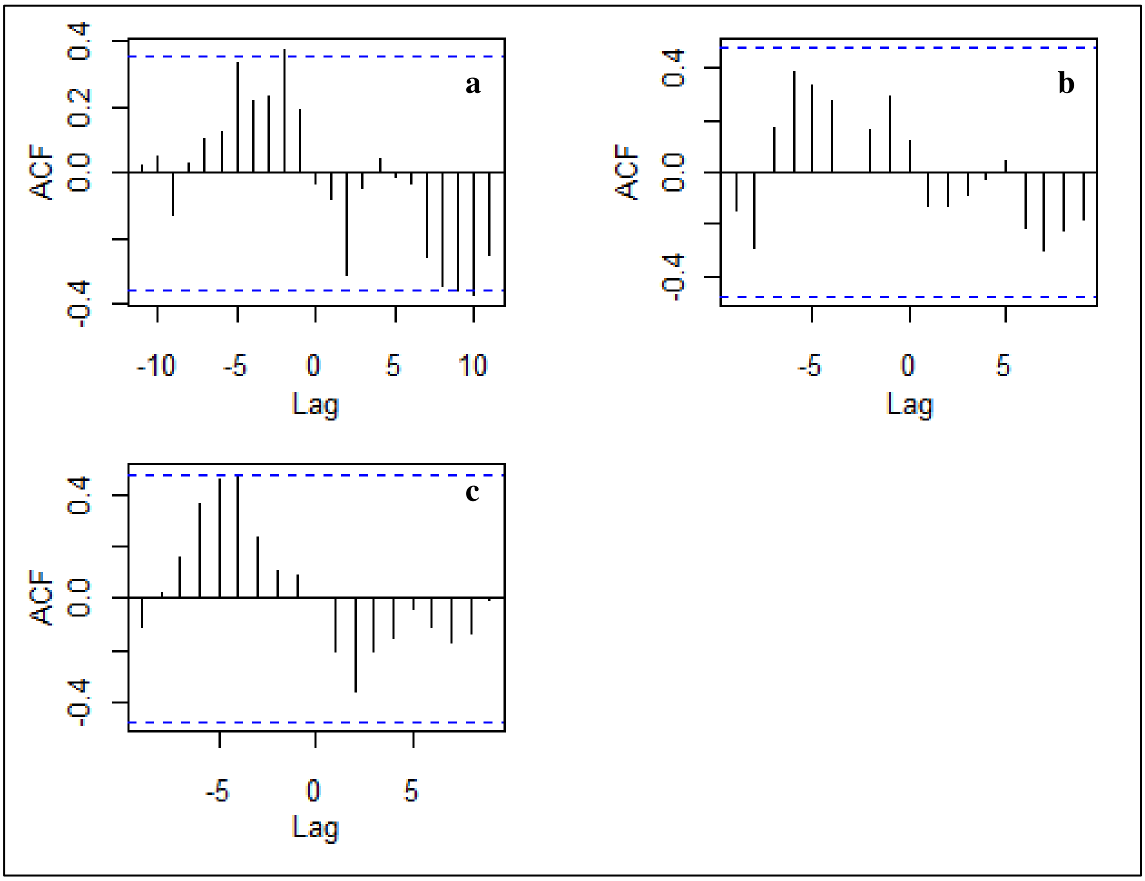


Figure 4.29. Correlograms of winter NAOI per year against a) RF returns, b) ICES PFA grilse and c) ICES PFA MSW; lag is years, dashed lines are significant at $\alpha = 0.05$.

The observed positive relationships in Fig. 4.29 may be an artefact of the few available data on returns and the broad scale over which the NAO is influential, as the numbers of returning salmon have been declining steeply while the wNAOI has largely been in a positive phase. In order to test whether the wNAOI had measurable effects on temporal $\delta^{13}C$ values of the salmon populations analysed here, as might be predicted due to the temperature-mediated determination of marine ecosystem $\delta^{13}C$ values, cross-correlations were run between wNAOI and the $\delta^{13}C$ values of each cohort from the River Frome and Northeast Coast population. Results are shown in Fig. 4.30.

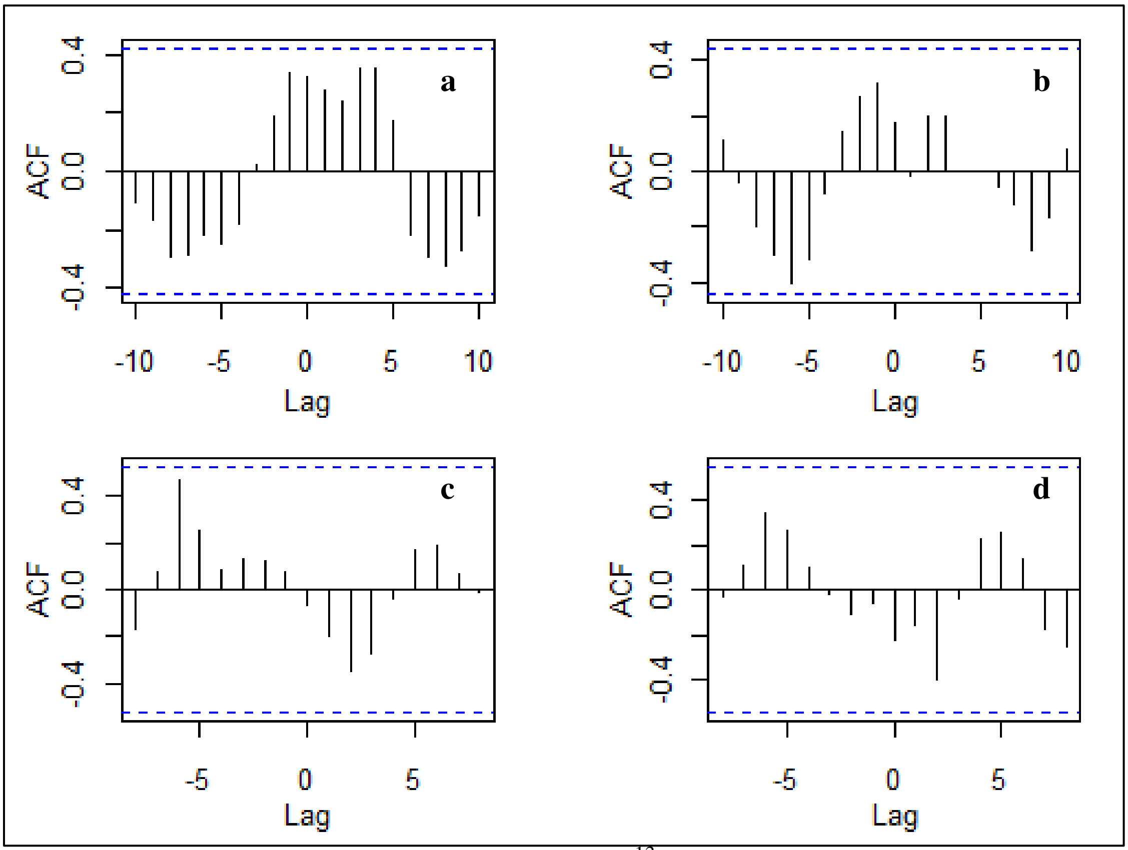


Figure 4.30. Correlograms of winter NAOI and $\delta^{13}C$ values per year for a) RF grilse, b) RF MSW fish, c) NEC grilse and d) NEC MSW fish; lag is years, dashed lines are significant at $\alpha = 0.05$.

No significant relationship is apparent between wNAOi and $\delta^{13}C$ values for any of the cohorts analysed here (see Fig. 4.30). There is, however, apparent structure in the cross-correlation data for each population cohort, indicating return periods of 11 (Fig. 4.30d), 12 (Fig. 4.26c), 14 (Fig. 4.30b) and >20 years (Fig. 4.30a), These results suggest some low-level control of $\delta^{13}C$ values by wNAOI, but it is likely that the major controls on these values are more localised given that the NAO operates on an ocean basin scale, while the salmon analysed here likely feed in relatively small and discrete regions of the North Atlantic.

As $\delta^{15}N$ values appear to be controlled in the majority by ecosystem processes and prey abundance, they might be expected to show similar relationships with wNAOI to those seem in the $\delta^{13}C$ data. The results of the $\delta^{15}N$ values to wNAOI cross-correlations are shown below in Fig. 4.31.

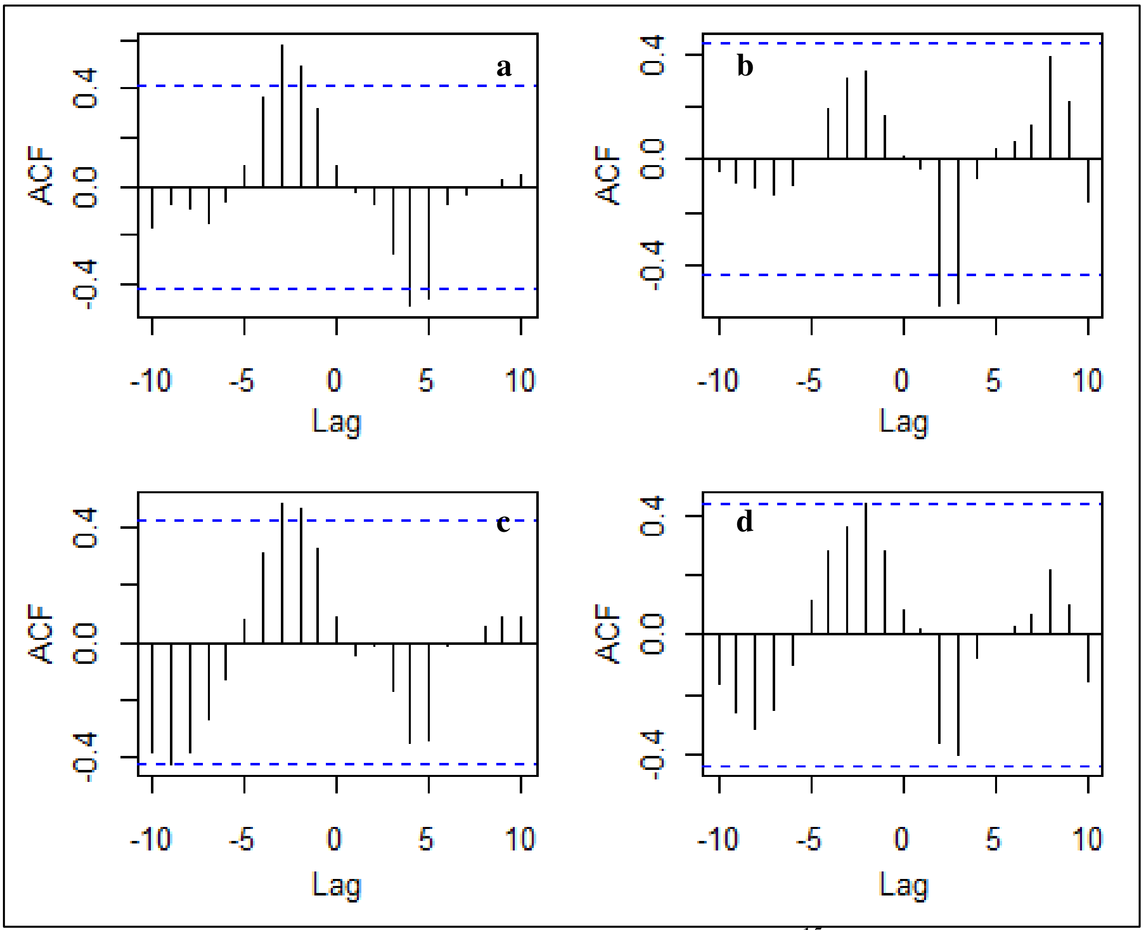


Figure 4.31. Correlograms of winter NAOI and a) RF grilse $\delta^{15}N$, b) RF MSW fish $\delta^{15}N$, c) RF grilse $\delta^{15}N'$ and d) RF MSW fish $\delta^{15}N'$; lag is years, dashed lines are significant at $\alpha = 0.05$.

Significant, positive correlations are seen between both uncorrected $\delta^{15}N$ (Fig. 4.31a) and mass corrected $\delta^{15}N'$ (Fig. 4.31c) against wNAOI for River Frome grilse, with a lag of minus two to three years, indicating that $\delta^{15}N$ values are highest two to three years after high wNAOI values. This relationship suggests that factors such as prey species abundance may be strongly linked to wNAOI, which warrants further investigation. Similar patterns are seen for MSW fish from this population, but no significant, positive relationship is seen between wNAOI and $\delta^{15}N$ values (Fig. 4.31b) until mass correction is applied (Fig. 4.31d), at which point there is a significant, positive relationship with a lag of minus two years, as seen in the grilse. Very similar negative trends are seen in both cohorts, pre- and post-mass correction, with a lag of plus two to five years, suggesting low $\delta^{15}N$ values a few years previous to high wNAOI values. Each return period in Fig. 4.31 is also similar, of between 10 to 14 years.

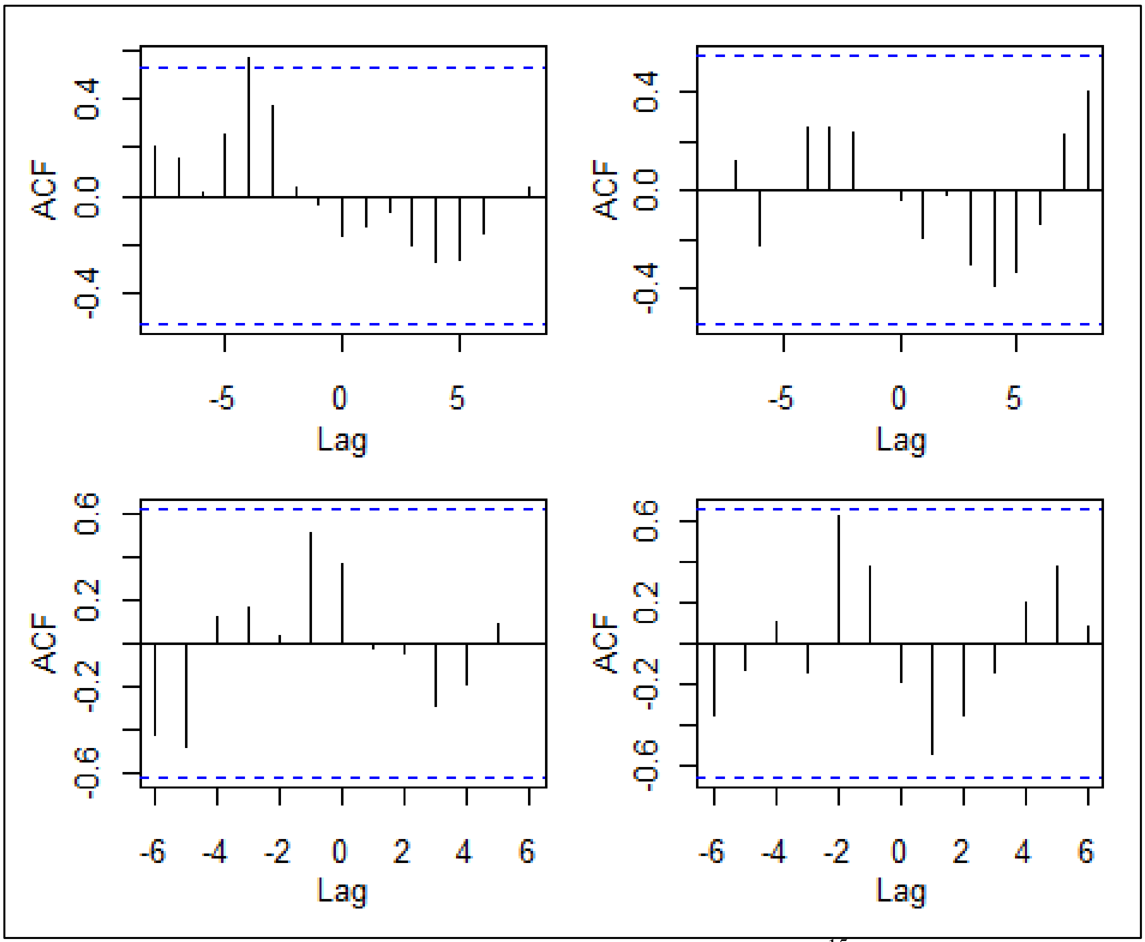


Figure 4.32. Correlograms of winter NAOI and a) NEC grilse $\delta^{15}N$, b) NEC MSW fish $\delta^{15}N$, c) NEC grilse $\delta^{15}N'$ and d) NEC MSW fish $\delta^{15}N'$; lag is years, dashed lines are significant at $\alpha = 0.05$.

There are suggestions of structure in the cross-correlations between the Northeast Coast grilse and MSW fish $\delta^{15}N$ values and wNAOI, but this structure is not as clear as seen in the River Frome plots above (Fig. 4.31). The only significant, positive correlation seen in Fig. 4.32 is in the $\delta^{15}N$ cross-correlation for Northeast Coast grilse, with a lag of minus four years, suggesting high $\delta^{15}N$ values in these fish pre-mass correction four years after high wNAOI values. This relationship breaks down post-mass correction (Fig. 4.32c), suggesting a size-mediated trophic link between wNAOI values and grilse $\delta^{15}N$ values four years later. There are no significant relationships with wNAOI for either mass corrected grilse $\delta^{15}N'$ values, or for MSW $\delta^{15}N$ values, either uncorrected or mass corrected (Fig. 4.32b&d), although there is the suggestion of a seven to 12 year return period in these cohorts, but the data are too sparse in these cross-correlations to make robust interpretations.

The links between returning numbers of salmon, $\boldsymbol{\delta^{13}}$C values and $\boldsymbol{\delta^{15}}$N values are intriguing, but are largely weaker than those seen within and between the stable isotope values, returns numbers and mass, so are likely a small controlling component in the dynamics of these variables compared to effects localised to specific feeding grounds. Further investigation is, however, warranted on more populations of salmon, but it seems likely that climate indices such as the NAO are too broadscale to exert major influence on the dynamics of salmon populations and cohorts showing marine feeding ground philopatry.

5. Location of feeding grounds

Sea surface temperature values directly and indirectly control the composition of carbon isotope values in phytoplankton at the base of the marine food chain (Barnes et al. 2009; Vander Zanden & Rasmussen 1999), which are dependent on the concentration of aqueous CO_2 in seawater, salinity, light intensity and plankton growth rates. These variables are either directly or indirectly related to SST (Hofmann et al. 2000; Popp et al. 1989; Rau et al. 1996; Switzer et al. 2003; Tamelander et al. 2009; Vander Zanden & Rasmussen 1999), and the baseline signature they produce is propagated up the food chain and integrated into salmon tissues with minimal trophic level fractionation (Hutchinson & Trueman 2006), as discussed in section 3.3. The Atlantic salmon scale isotope values investigated here represent the integrated isotopic values from approximately eight months of feeding over a summer season; small spatial, temporal and taxonomic differences in the carbon isotope composition of the food web during this period are likely to be insignificant when compared to the SST-related basal ecosystem signature. Hence, differences in $\delta^{13}C$ values between groups of salmon over the last season of growth indicate disparities in conditions experienced at sea over the full summer of growth, and therefore separation in marine location.

As baseline marine ecosystem $\delta^{13}C$ values are strongly related, both directly and indirectly, to sea surface temperature (SST), relationships between scale $\delta^{13}C$ values during the last season of marine growth and SST during the same time period may logically be used to locate Atlantic salmon at sea. A similar methodological approach has previously been used to identify the wintering area used by Danish barn swallows in South Africa (Szép et al. 2006). The area was identified using a correlation between adult survival and an index of vegetation, the Normalised Difference Vegetation Index (NDVI – an index of habitat condition, based on satellite observations), where the NDVI in a specific location during March to May of the year explained a large proportion of the variation in annual adult survival, and was therefore taken as the wintering area.

The marine ecosystem has highly dynamic baseline isotopic values, both spatially and temporally. On an oceanic scale, $\delta^{13}C$ values in the Atlantic have a latitudinal gradient, with the highest levels of enrichment in warm, tropical areas (Graham et al. 2010; Hofmann et al. 2000; Lara et al. 2010; Rubenstein & Hobson

2004). At a finer scale, such as that of areas used by Atlantic salmon as feeding grounds, the broad brush isoscape (spatially explicit patterns of isotope variation, or isotope landscapes) patterns are broken down by variations in primary production between seasons, years and areas (Barnes et al. 2009; Lara et al. 2010; Wainright et al. 1993). The highly variable nature, therefore, of baseline $\delta^{13}C$ values at a scale relevant to fish such as salmon means that a single, isoscape type of relationship between $\delta^{13}C$ values and SST across all potential feeding grounds within the North Atlantic would simply not work.

To determine the likely location of open ocean feeding areas for our sample salmon populations, the temporal covariance between LOESS-smoothed scale $\delta^{13}C$ values within each cohort and SST was assessed by linear regression in each one-degree grid square between 45-75°N latitude and 65°W-20°E longitude for the period 1985 to 2002 (Rayner et al. 2003; UK Meteorological Office Hadley Centre 2006). This area corresponds roughly to the region of sea thought to be suitable oceanic thermal habitat for Atlantic salmon (Parrish et al. 1998; Spares et al. 2007). Coefficients of variation (R^2 values) between LOESS-smoothed annual scale collagen $\delta^{13}C$ values for the last season of growth and median March to October SST data for each year taken from the HADISST dataset (Rayner et al. 2003; UK Meteorological Office Hadley Centre 2006) were calculated per one degree grid square within this rectangle of the North Atlantic. These R^2 values were then mapped using ESRI® ArcGIS™ software, to display the areas of highest correlation between interannual variations in $\delta^{13}C$ values and in SST. Data were converted into georeferenced points with latitude and longitude values (one R^2 value per degree, $n = 1869$ per cohort), and interpolated by kriging, using a spherical semivariogram model, to produce a display format for the data. The maps are projected in the WGS84 (World Geodetic System 1984) datum, which is the same coordinate system used by the Global Positioning System (GPS) (Rossbach 2000).

Time series of tissue isotopes and SST are autocorrelated, violating the assumptions of serial independence demanded by most classical inference tests. Autocorrelated time series are frequently de-trended to remove underlying low-frequency variations, however this research is primarily interested in low frequency variations that are common to both time series, thus de-trending would be counter-productive. Instead, the influence of high frequency fluctuations in the time series was reduced by applying LOESS smoothing with a span of 0.5 and polynomial order 2, as discussed in Chapter 4. Low frequency variations in the smoothed time series were correlated, and the influence of autocorrelation on significance tests was accounted for by adjusting the effective degrees of freedom for each time series pair using the modified Chelton method (Pyper & Peterman 1998). Areas with the highest correspondence between temporal variations in SST and measured $\delta^{13}C$ values are suggested as the most likely marine feeding areas during deposition of scale collagen (Figs 5.1, 5.3, 5.5 & 5.7).

The correlation approach taken here is based on the LOESS smoothed fit, and is sensitive to within-year variance, i.e. the assumption that all fish sampled return from the same location at sea. The effect of within-year variance in $\delta^{13}C$ values was also tested by removing all years where within-year $\delta^{13}C$ standard deviations exceeded 5% of the mean value for that year. This threshold was chosen to be similar to the threshold accepted for analytical precision. Two years were removed from the River Frome grilse data, one from the River Frome MSW data, four from the North East Coast grilse data and three from the Northeast Coast MSW data. Removing years of high variance did not have a dramatic effect on the proposed feeding grounds, but increased the strength of correlations (Figs 5.2, 5.4, 5.6 & 5.8).

5.1 River Frome grilse and MSW fish

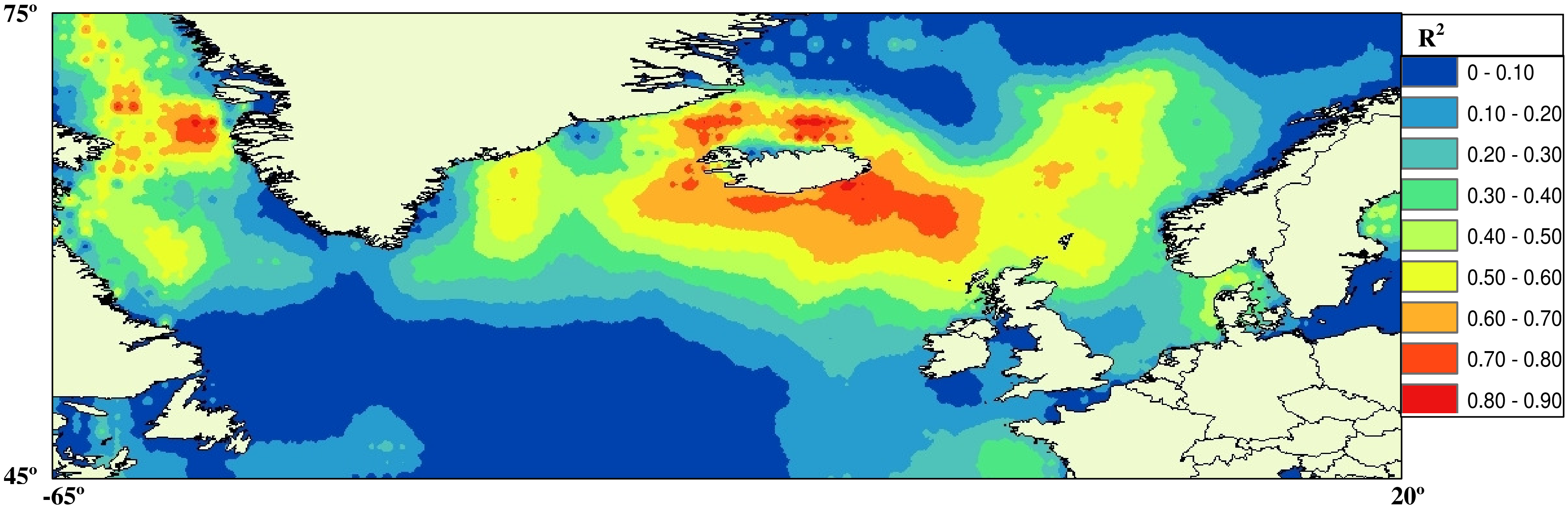


Figure 5.1. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale δ^{13}C values for River Frome grilse and annual median eight month SST (March to October, inclusive), from 1985 to 2002 in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

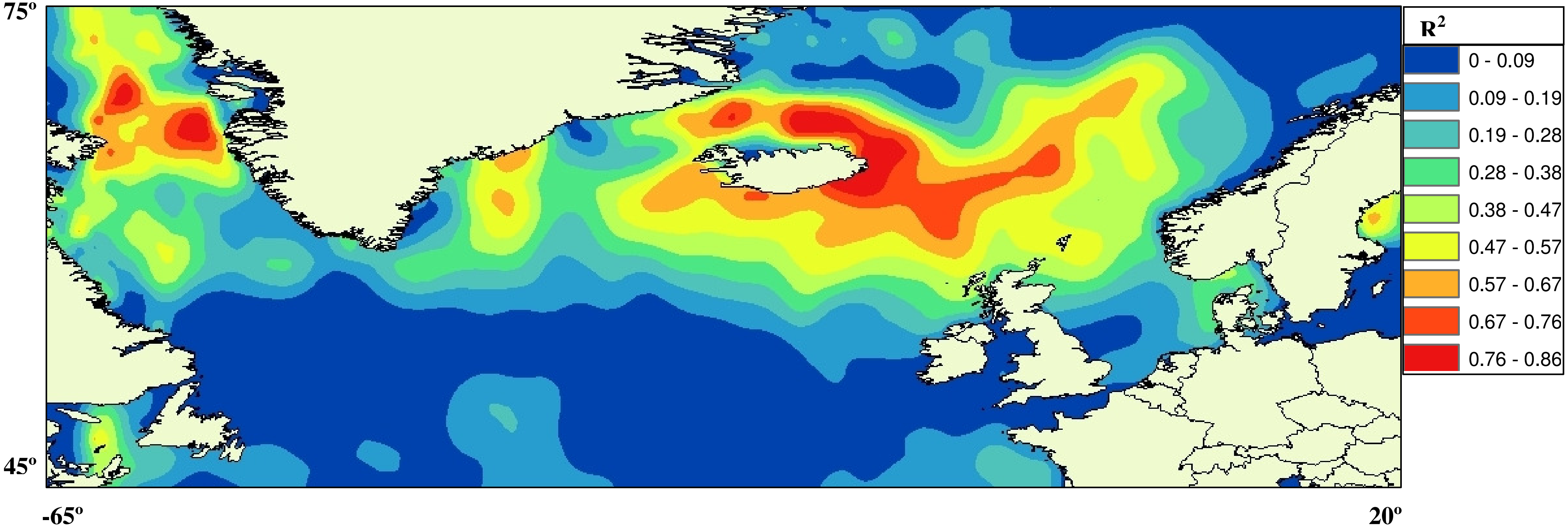


Figure 5.2. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for River Frome grilse and annual median eight month SST (March to October, inclusive), from 1985 to 2002 (with years of SD > 5% of the mean for that year removed), in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

The map in Fig. 5.1 shows R^2 values between variation in LOESS-smoothed annual $\delta^{13}C$ values for River Frome grilse scales and variation in annual median values for SST between March and October, inclusive, for the years 1985 to 2002, interpolated to produce a continuous spatial representation of the strength of these R^2 values. The map in Fig. 5.2 shows the same correlations, but with years removed where the standard deviation of the $\delta^{13}C$ values exceeded 5% of the mean for that year for River Frome grilse $\delta^{13}C$ values (1987, 1997); this removal strengthens the correlations around the northeast of Iceland and northwest of the Faroes, delineating a likely are of salmon marine habitat.

The highest R^2 values in Figs 5.1 and 5.2 are around the north and east edges of the Icelandic Continental Shelf at approximately -10º to -13ºW and 68ºN. This area has high levels of upwelling, which lead to concentration of nutrients in this region (Corten & Lindley 2003; ICES 2009a); the elevated nutrient concentrations lead to aggregations of phyto- and zooplankton, which in turn make it important as a spawning ground and nursery for other pelagic fish, such as mackerel and blue whiting (Corten 2001; Corten & Lindley 2003; ICES 2009a; Jacobsen & Hansen 2001), which are important food sources for Atlantic salmon at sea (Haugland et al. 2006; ICES 2009a; Jacobsen & Hansen 2001). It is logical that salmon would use an area of high productivity as a feeding ground. This area is situated in the likely migration path from the River Frome along the western branch of the North Atlantic, see Fig. 1.3, meaning that salmon may thus become habituated to return to this area in the same way as they return to their natal streams to spawn. The location of this proposed feeding ground suggests that River Frome grilse exit the western outflow of the English Channel and join the North Atlantic Current (see Fig. 1.3), which would carry them to the feeding ground, and potentially beyond. This is broadly consistent, in terms of direction travelled, with the "Merry-Go-Round" hypothesis (Dadswell et al. 2010), which suggests that salmon migrate along the currents of the North Atlantic Subpolar Gyre, although the grilse travelling distance suggested by this hypothesis seems unlikely given their short marine life history and rate of migration (Booker et al. 2008; Holm et al. 2003). It seems likely that the River Frome grilse would not migrate far beyond the rich feeding grounds on the Icelandic Shelf breaks, as they return to their natal rivers after approximately one to 1.5 years at sea (Welton et al. 1999), potentially continuing their journey only as future MSW fish. The short time before return makes the high correlations to the west of Greenland unlikely feeding areas for this cohort.

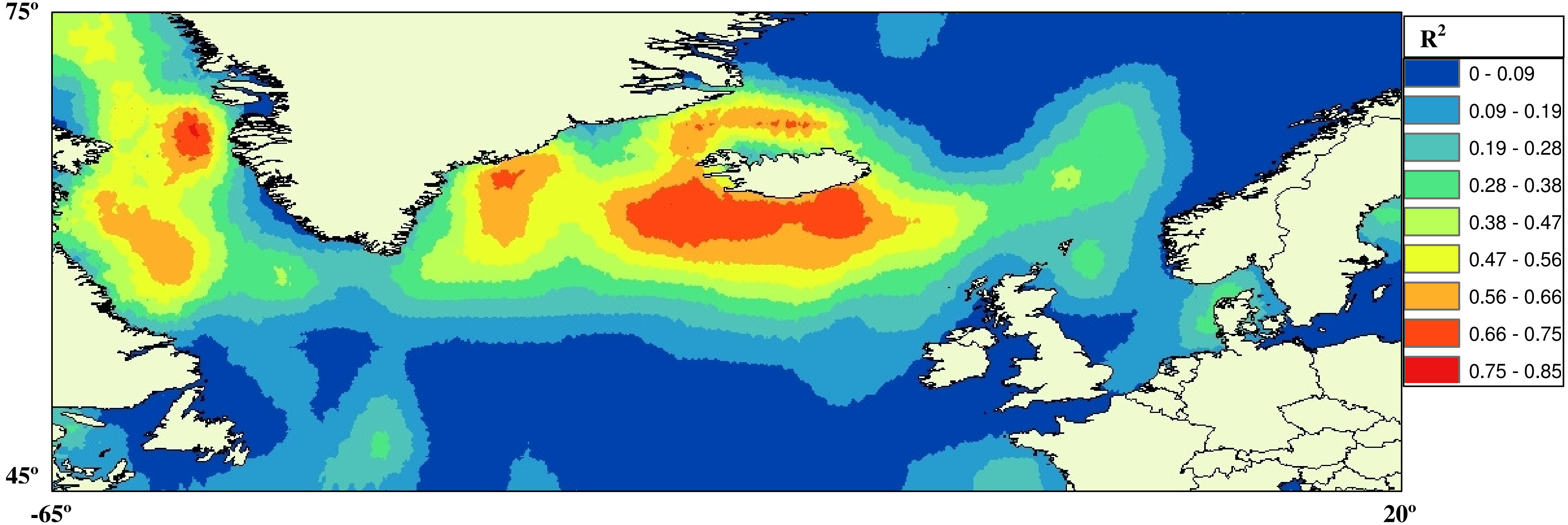


Figure 5.3. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS-smoothed annual mean scale $\delta^{13}C$ values for River Frome MSW fish and annual median eight month SST (March to October, inclusive), from 1985 to 2002 in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

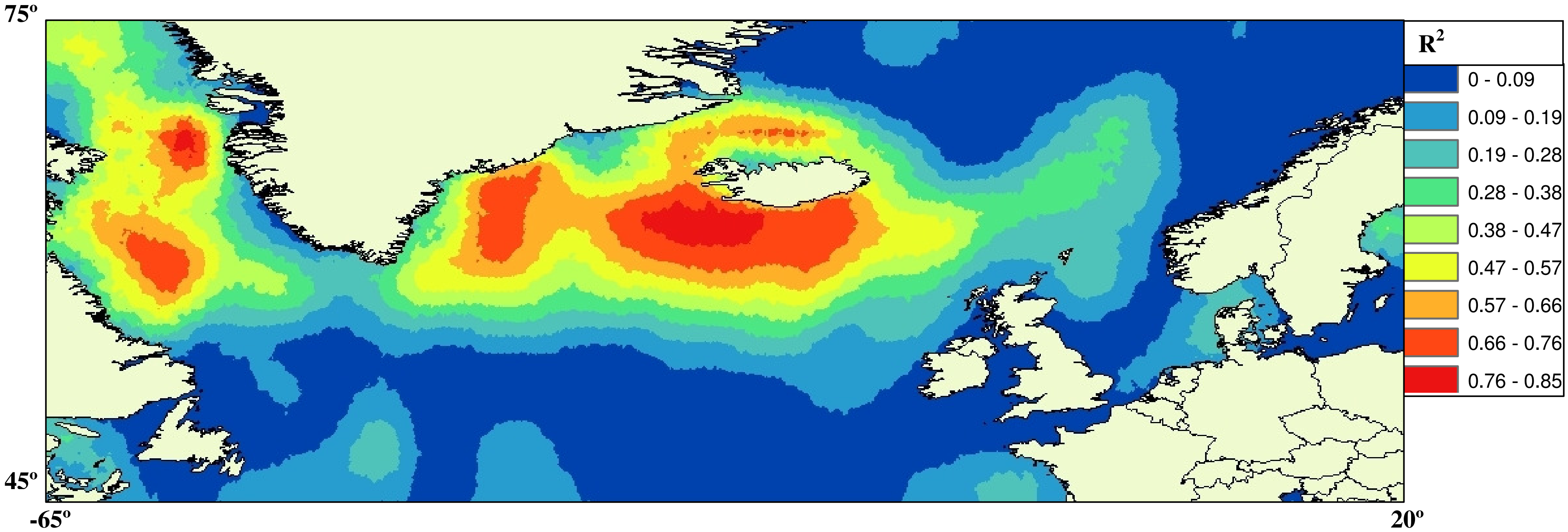


Figure 5.4. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for River Frome MSW fish and annual median eight month SST (March to October, inclusive), from 1985 to 2002 (with years of SD > 5% of the mean for that year removed), in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

The map in Fig. 5.3 shows R^2 values between variation in LOESS-smoothed annual $\delta^{13}C$ values for River Frome MSW salmon scales and variation in annual median values for SST between March and October, inclusive, for the years 1985 to 2002, interpolated to produce a continuous spatial representation of the strength of these R^2 values. The map in Fig. 5.4 shows the same correlations, but with years removed where the standard deviation of the $\delta^{13}C$ values exceeded 5% of the mean for that year for River Frome MSW fish $\delta^{13}C$ values (1994); this removal further strengthens the correlations around the south-west Icelandic Shelf break.

The areas with the highest correlations between variation in $\delta^{13}C$ values and SSTs are to the south of Iceland, particularly to the south-west, in the region of the Icelandic Shelf break, centred around -24ºW and 62ºN, and in the Labrador Sea between Canada and West Greenland, with the highest correlations centred around -56ºW and 66ºN, and -58ºW and 59ºN. The areas of highest correlation are all coincident with areas of high upwelling of nutrients on shelf breaks (Williams & Follows 1998). These proposed feeding grounds for River Frome MSW salmon have enhanced conditions for production caused by shelf edge currents concentrating nutrients at the edges of the shelf breaks (Genin 2004; White et al. 1998). The concentration of nutrients in these regions leads, as with the shelf break to the north of Iceland, to enhanced conditions of primary production (Waser et al. 2000; White et al. 1998), and therefore to aggregations of forage fish such as herring, capelin and blue whiting (Holst et al. 1998; ICES 2009a). MSW fish have considerably more time at sea, as their name suggests, meaning that they can migrate further north or west than grilse to cooler, more productive areas of sea in which feeding and growth are easier, with lower metabolic demands than in warmer southern waters (Cunjak et al. 2005; Jákupsstovu 1988; Todd et al. 2008). Importantly for the feeding grounds postulated based on these maps, there is a logical migration path between the potential grilse feeding ground around the north and east of Iceland and the areas of high correlation to the south and west, following the direction of the prevailing Irminger current (Poulain et al. 1996). If the MSW component of this population were to spend its 1+ (growth after the first sea-winter) season at sea around the north and west of Iceland with the fish that return as grilse, they could subsequently migrate clockwise around Iceland using the Irminger Current or west of Greenland using the North Atlantic Drift Current (Bacon 1997) towards the potential feeding areas suggested in the Labrador Sea for their subsequent season(s) of growth (see Figs 5.3 & 5.4).

Discussion of maps for River Frome grilse and MSW fish

There is, as confirmed by the temporal trends in $\delta^{13}C$ values (chapter 4), a strong spatio-temporal separation between the cohorts of grilse and MSW salmon from the River Frome archive for the time covered by these analyses. This segregation indicates one of two things: either the Frome population has a genetic component that may divide it into cohorts on initial migration whence each goes directly to different areas in the sea, or these salmon occupy two summer feeding grounds: north and east of Iceland during the second growth season at sea (see Figs 5.1 & 5.2), and the south west Iceland/West Greenland areas in the subsequent season(s) (see Figs 5.3 & 5.4). It is interesting to note that both cohorts appear to be using areas of similar oceanographic conditions, i.e. at shelf breaks, with strong upwelling currents, high primary productivity and aggregations of favoured prey items. The mapped R^2 values identify regions of the Atlantic that might be logically chosen as favourable Atlantic salmon habitat based on environmental conditions and prey availability, and are on logical migration trajectories based on time at sea and ocean currents. The possibility therefore exists that the salmon surviving to return, from which the samples are drawn, are the fish that successfully migrate to these productive shelf break areas of the Atlantic Ocean. Neither map shows the highest correlation values in traditional fishery areas, thus it is difficult to validate the conclusions drawn here. Given that the fisheries only sample in fishery areas, and that numbers of tagged fish caught are minimal, the indirect evidence, given by temperature-controlled isotopic variation, is compelling.

5.2. Northeast Coast grilse and MSW fish

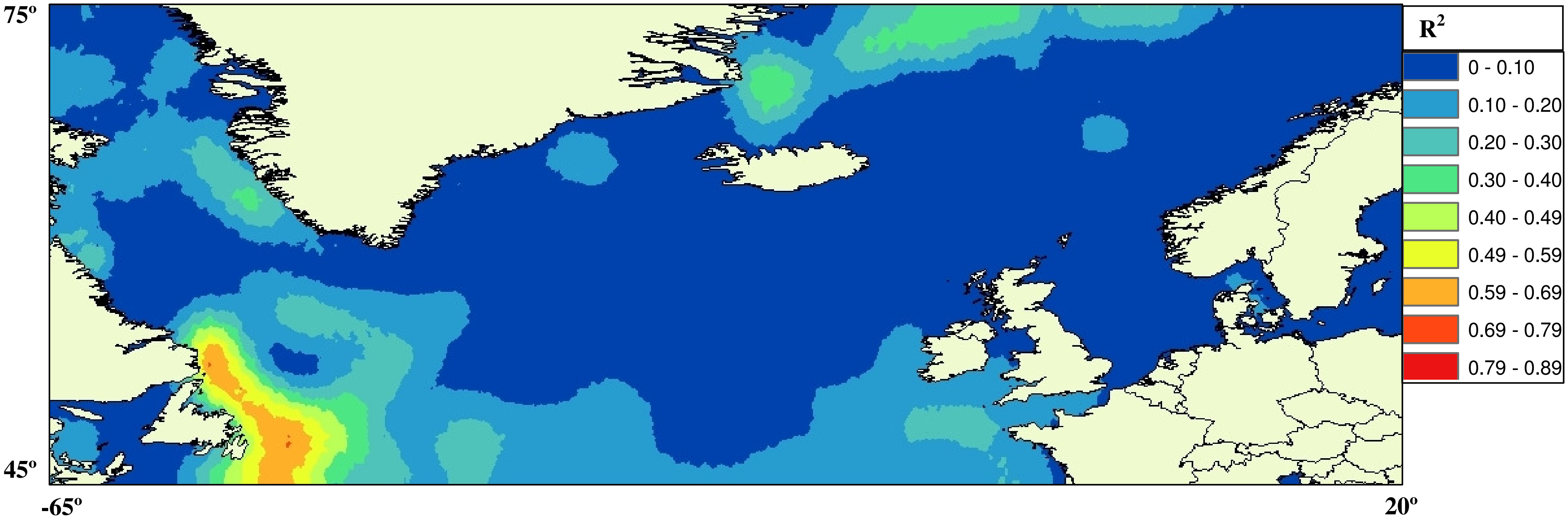


Figure 5.5. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for Northeast Coast grilse and annual median eight month SST (March to October, inclusive), from 1985 to 2002 in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

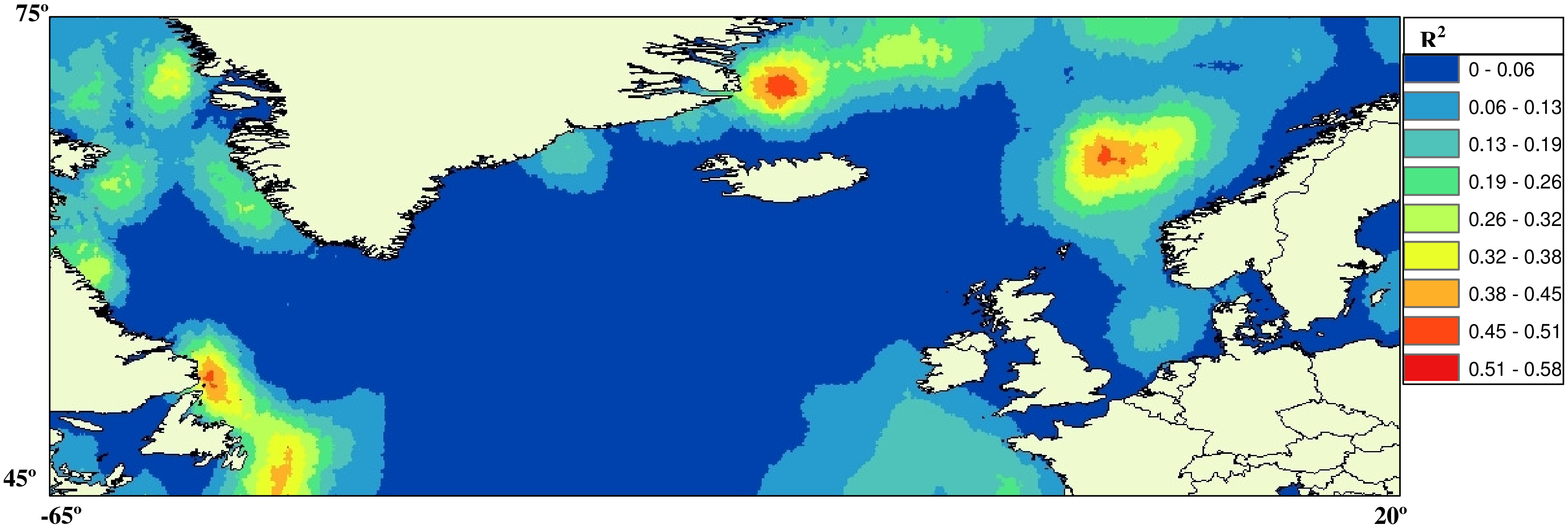


Figure 5.6. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for Northeast Coast grilse and annual median eight month SST (March to October, inclusive), from 1985 to 2002 (with years of SD > 5% of the mean for that year removed), in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

The map in Fig. 5.5 shows R^2 values between variation in LOESS-smoothed annual $\delta^{13}C$ values for Northeast Coast grilse scales and variation in annual median values for SST between March and October, inclusive, for the years 1985 to 2002, interpolated to produce a continuous spatial representation of the strength of these R^2 values. The map in Fig. 5.6 shows the same correlations, but with years removed where the standard deviation of the $\delta^{13}C$ values exceeded 5% of the mean for that year for Northeast Coast grilse $\delta^{13}C$ values (1985, 1987, 1989, 2001); this removal produces observable feeding ground hypotheses in the strong correlations within the Norwegian Sea and north of Iceland.

The highest R^2 values are to the north of the Shetland Isles and northeast of the Faroe Islands, in the Norwegian Sea at approximately 1.5ºE and 66ºN, on the edge of the Norwegian Current frontal zone and near the Norwegian Continental Shelf break, and around 19ºW and 71ºN to the east of Greenland at the edge of the Jan Mayen fracture zone near the Greenland Shelf break. These areas, as with the putative feeding areas for both of the River Frome cohorts, has high levels of nutrients due to frontal zone concentration effects in this region (Kostianoy & Nihoul 2009). The areas are rich in forage fish, particularly Norwegian spring spawning herring, mackerel and blue whiting (Haugland et al. 2006; Holst et al. 1998; ICES 2009a), which are preferred prey items for Atlantic salmon at sea (Haugland et al. 2006; Jacobsen & Hansen 2001). Both areas are situated in the likely migration path from the Northeast Coast to the Norwegian Sea and onwards, exiting at the north end of the North Sea and using the Slope then Norwegian Atlantic Currents to travel north- and westwards to the feeding grounds. Because there is are strong correlations in this cohort between $\delta^{13}C$ values and returns, the ocean climate conditions in the region used for feeding should exert a strong control on numbers of returning grilse. This relationship allows for a potential test of the putative Northeast Coast grilse feeding ground location, where future ocean climatic conditions within these regions should show a relationship with future numbers of grilse returning to this population.

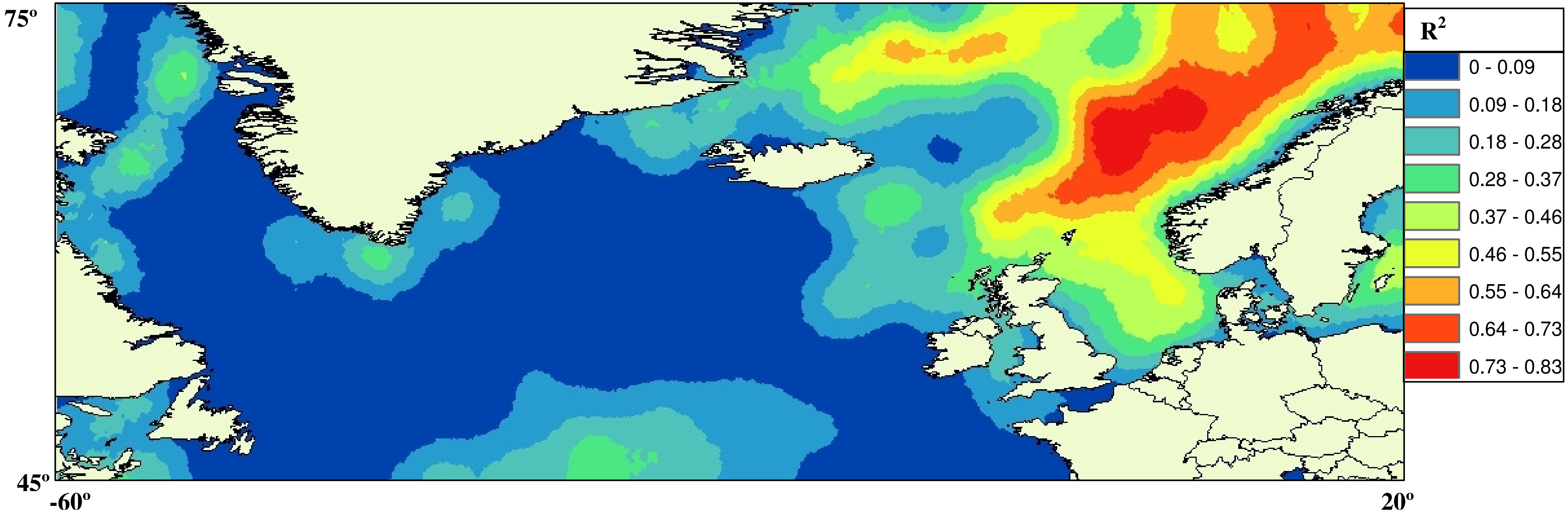


Figure 5.7. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for Northeast Coast MSW fish and annual median eight month SST (March to October, inclusive), from 1985 to 2002 in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

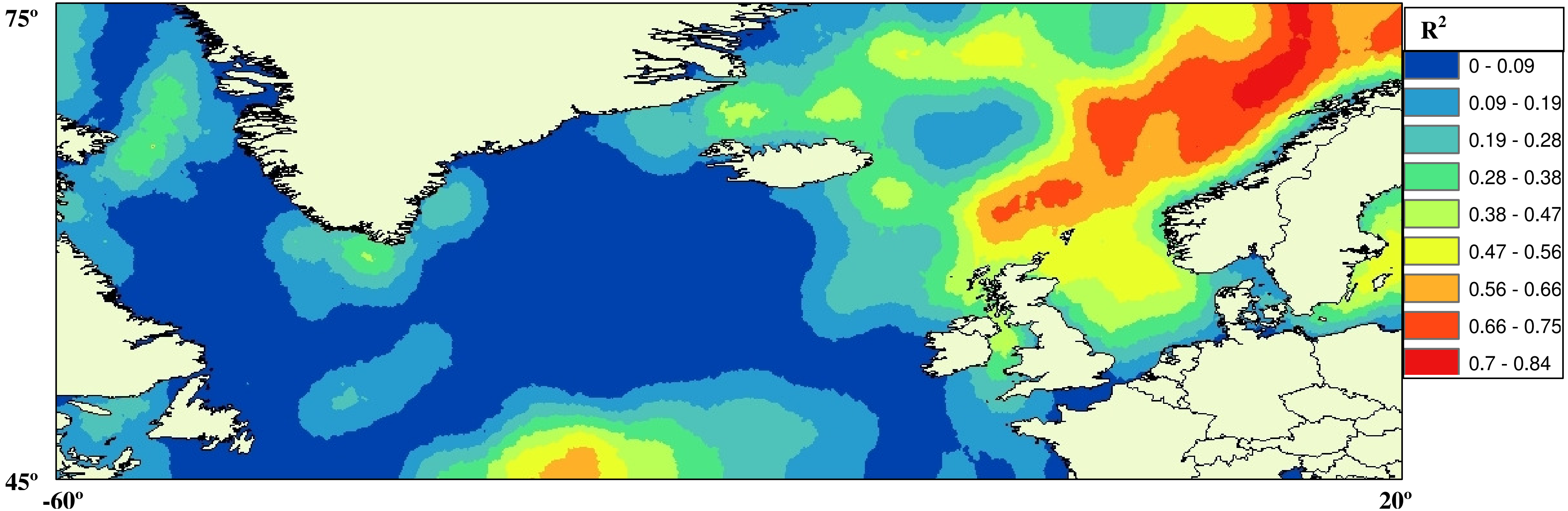


Figure 5.8. Map of interpolated coefficients of variation (R^2 values) strengths between LOESS–smoothed annual mean scale $\delta^{13}C$ values for Northeast Coast MSW fish and annual median eight month SST (March to October, inclusive), from 1985 to 2002 (with years of SD > 5% of the mean for that year removed), in each one degree grid square between -65ºW to 20ºE and 45ºN to 75ºN in the North Atlantic. The colour coded key gives R^2 values.

The map in Fig. 5.7 shows R^2 values between variation in LOESS-smoothed annual $\delta^{13}C$ values for Northeast Coast MSW salmon scales and variation in annual median values for SST between March and October, inclusive, for the years 1985 to 2002, interpolated to produce a continuous spatial representation of the strength of these R^2 values. The map in Fig. 5.8 shows the same correlations, but with years removed where the standard deviation of the $\delta^{13}C$ values exceeded 5% of the mean for that year for Northeast Coast MSW fish $\delta^{13}C$ values (1985, 1986, 1989); this removal narrows the are of strong correlations within the Norwegian Sea.

The highest R^2 values are at approximately 12-13ºE and 69-74ºN, to the south and west of Bear Island between the Norwegian mainland and Svalbard, in the north Norwegian Sea near the Barents Sea border. This area of high correlations is situated in the main warm water current from the Atlantic and near the continental shelf break of the Bear Island Trough. This is a highly productive area, with large phytoplankton blooms leading to high densities of pelagic prey items preferred by Atlantic salmon including euphausiids, capelin, herring and blue whiting (ICES 2009a; IMR/PINRO 2006). It is interesting to see that the putative feeding area is in the Arctic, but in a warm Atlantic current that maintains temperatures at a level acceptable to the Atlantic salmon. The warm current also contributes to the highly productive nature of this region. There is a logical migration path between the potential grilse feeding ground in the southern Norwegian Sea and the area of high correlation seen in Fig. 5.8 in the northern Norwegian Sea, which adds weight to the hypothesis that Northeast Coast grilse feed in the Norwegian Sea rather than off East Greenland. Were the MSW component of this population to spend its 1+ (growth after the first sea-winter) season at sea in the south with the fish that return as grilse, these fish could subsequently migrate northwards to the potential MSW feeding ground using the same Norwegian Current branch of the North Atlantic Current that continues further north through the potential grilse feeding grounds towards Svalbard to Greenland (see Fig. 1.3). There is a significant correlation in this cohort between $\delta^{13}C$ values and returns, meaning that the ocean climate conditions in this region should, as suggested for grilse from this population, exert a strong control on numbers of returning MSW salmon. Again, this relationship allows for a potential test of the putative Northeast Coast MSW fish feeding ground location, where future ocean climatic conditions within this region should show a strong relationship with future numbers of MSW fish returning to this population.

Discussion of maps for River Frome grilse and MSW fish

There is, as shown by the temporal trends in $\delta^{13}C$ values (chapter 4), no strong spatio-temporal separation between the cohorts of grilse and MSW salmon from the Northeast Coast archive for the time covered by these analyses. There are, however, minor, non-significant inter-annual differences in mean carbon isotope values between the cohorts, which lead to the geographic separation evident in Figs. 5.5 & 5.6, and 5.7 & 5.8. These small differences create slightly different patterns of temporal variation in $\delta^{13}C$ values for each age class, which means that the strongest correlations with temporal SST variations are in slightly different areas. As the patterns in mean $\delta^{13}C$ values of grilse and MSW salmon are similar overall, however, it might be expected that the areas of strongest correlations with SST variations would be relatively local to one another, as SST values exhibit continuous rather than discrete variations throughout the oceans. This is clearly the case, as the most likely grilse feeding area is in the southern Norwegian Sea, while MSW salmon appear to be feeding in the northern Norwegian Sea, further away from their point of origin. In this population it seems unlikely that cohorts are divided, based on a genetic component, on initial migration, but that these salmon occupy two summer feeding grounds: the southern Norwegian Sea during the second growth season at sea (see Fig. 5.6), and the northern Norwegian Sea in the subsequent season(s) (see Fig. 5.8). As with the potential feeding grounds for the River Frome population, both cohorts appear to be using areas of similar oceanographic conditions, i.e. near to shelf breaks, with strong upwelling currents, high primary productivity and aggregations of favoured prey items. The mapped R^2 values again identify regions of the Atlantic that might be logically chosen as favourable Atlantic salmon habitat based on environmental conditions and prey availability, and are on logical migration trajectories based on time at sea and ocean currents. The possibility therefore exists that the salmon surviving to return, from which the samples are drawn, are the fish that successfully migrate to these productive shelf break areas of the Atlantic Ocean. The putative feeding grounds identified by the maps are fished, but generally for densely shoaling pelagic fish such as herring, rather than for salmon (Holst et al. 1998; ICES 2009a). It might be possible to validate the conclusions drawn here if the existing fisheries were monitored for salmon catches, but this would be reliant on the capture of tagged individuals with recorded stock identities, which are rarely found (ICES 2009c). As with the River Frome salmon, the indirect evidence for feeding locations, given by temperature-controlled isotopic variation, is compelling.

5.3. Comparison of River Frome and Northeast Coast maps

The maps produced for grilse and MSW salmon from the two populations investigated here show some interesting results; the potential feeding grounds identified for all four groups of fish are in highly productive areas with abundances of preferred prey species. Moreover, the putative grilse feeding grounds are on logical migration routes between their rivers of origin and the feeding grounds of the MSW fish, using the prevailing North Atlantic oceanic currents.

It is assumed that each population uses the same feeding grounds throughout the time covered by this study. For each cohort within each population, the within-year variations about the mean $\delta^{13}C$ values are significantly lower than the total variance. If the fish within the cohorts were separated in the open ocean, they would experience different ecosystem baseline $\delta^{13}C$ values, and the variance about the mean annual values would be relatively large. The relatively lower variance in annual $\delta^{13}C$, when compared to the total population variance, indicates that all of the fish in each cohort are likely to be in an area with similar baseline $\delta^{13}C$ values each year. For the Northeast Coast cohorts, the inter-annual patterns of variation seen are continuous from the preceding year, with periodic, cyclical trends clear in both grilse and MSW fish. If the fish were not using the same areas year after year, the variance within individual years might remain relatively low, but the cycles would break down, showing a pattern of random $\delta^{13}C$ values relative to the preceding and following years. For the River Frome cohorts, the inter-annual variations are significantly smaller than seen in the Northeast Coast cohorts; it is possible that the Frome salmon track areas of sea with preferred baseline ecosystem conditions, and therefore maintain relatively similar $\delta^{13}C$ values on an inter-annual basis. For this to be the case, however, each River Frome cohort would need to move as a closely schooling group throughout the open ocean every year, or the intra-year variation would be considerably higher. Based on patterns in intra- and inter-annual variation discussed, it seems logical to suggest that grilse and MSW fish from the River Frome and the Northeast Coast populations return year-on-year to population- and cohort-specific feeding grounds.

The stable isotope results presented here suggest that salmon returning to the River Frome and North East Coast do not feed in the traditional salmon fishing grounds. Since the late 1950s, a total of only 387 tagged salmon from England and Wales and 399 from Scotland have been recovered from around Greenland; these figures are even lower in the Faroes, with only 69 salmon from England and Wales and 135 from Scotland recovered (ICES 2007, 2009c). Given the millions of salmon that have been tagged in the British Isles (c. 3.5 million in England and Wales, total numbers not currently available for Scotland) and the low numbers of recaptures, it seems likely that many of the fish originating from the UK feed outside of the fishing areas around Greenland and the Faroe Islands where most of the recaptured tagged salmon have been caught. The recapture data are not currently available in any meaningful numbers broken down by river of origin, although a few individual river data points exist (ICES 2007). The overall recapture rates are so low on tagged salmon from England, however, that it is not currently possible to use these numbers to draw any meaningful conclusions about migration or feeding grounds that might be compared with suggested isotope-based feeding grounds.

It would be very interesting to monitor future climatic and ecosystem conditions in the feeding grounds proposed by these maps to determine whether these regions exert population- and cohort-specific controls on returning numbers of salmon.

6. Conclusions

Compared to the natural range of the Atlantic salmon, the natal rivers of the River Frome and the Northeast Coast populations of Atlantic salmon are relatively close geographically, but these two populations, and the cohorts therein, are quite different from one another in marine life history. The Frome population is a much smaller single river stock, with annual returns of approximately 500 to 1500 adult fish in recent years (CEH, unpubl. data), while the Northeast Coast salmon stem from several river stocks, with (using the River Tyne as an example) recent rod catch data alone of over 2000 fish annually (Environment Agency 2005b). Both populations, however, have been in decline over the past few decades (Hilton et al. 2001; Welton et al. 1999).

The River Frome is largely a spring-fed chalk stream in the south of England, which has been experiencing rising temperatures over the past two decades (Arnott et al. 2009; Bowes et al. 2005; Durance & Ormerod 2009; Mackey & Berrie 1991), while the Northeast Coast population stems from rainwater-fed rivers flowing off the hills in the northeast of England and southern Scotland (Environment Agency 2005a; Williams et al. 2008a). Grilse in both populations constitute the majority of the adult returning fish (Beaumont et al. 2009; Environment Agency 2005b; Welton et al. 1999). This Northeast Coast population feeds into the North Sea and then to the North Atlantic, while the River Frome population migrates out into the English Channel, from where it likely heads west, joining the Atlantic to the south of Ireland, meaning that these populations have quite distinct out-migration pathways to their feeding grounds. The early-life ecology and native stream habitats are quite different in these two populations, despite their relative proximity; it is therefore likely that their behaviour at sea might show some population-based differences.

6.1. Comparison of δ^{13}C values

Salmon from the River Frome show significant separation between grilse and MSW cohorts in δ^{13}C values, as discussed in chapter 3 (see Table 3.2 for ANOVA results), with significantly elevated values in grilse. This relative enrichment in grilse ^{13}C is contrary to what would be expected were these signals trophic, meaning that they must be strongly related to isotopic conditions at the base of the food chain. The negative relationships between δ^{13}C values and mass for both cohorts are further evidence that δ^{13}C values are not controlled by trophic enrichment. The elevation in grilse $\delta^{13}C$ values and the overall separation between the two Frome cohorts indicates that they are experiencing significantly different ecosystem baseline conditions during their last marine feeding season. As the scale tissues sampled represent the integrated isotopic dietary signal for the entire last season of growth (taken as approximately the eight month period between March and October) for each fish, different baseline conditions imply different feeding locations at sea.

Northeast Coast grilse and MSW salmon, in contrast to the Frome cohorts, show no significant separation in $\delta^{13}C$ values, as discussed in chapter 3 (see Table 3.2 for ANOVA results). It is unlikely, that $\delta^{13}C$ values are trophically controlled in either cohort, as there is no significant relationship with mass. With control of $\delta^{13}C$ values through trophic level enrichment, the much larger MSW fish should be isotopically heavier relative to the grilse; this indicates that ecosystem baseline conditions likely exert the strongest control on $\delta^{13}C$ values. The lack of overall separation between the two cohorts suggests that they are experiencing similar baseline ecosystem conditions during their last season of marine growth, implying that they are feeding in similar areas at sea.

River Frome mean salmon scale $\delta^{13}C$ values are relatively stable and invariant through time for both cohorts compared to the Northeast Coast cohorts. The separation in $\delta^{13}C$ values is maintained throughout almost every year sampled between 1971 and 2002, see Fig. 4.1. The relatively low intra-annual variances, together with the comparatively flat patterns in annual mean $\delta^{13}C$ values through time, imply that the baseline $\delta^{13}C$ values over the time covered by these analyses are relatively stable in the feeding grounds. This stability suggests that returning numbers of fish are unlikely to show a relationship with $\delta^{13}C$ values, and thus ocean climate conditions in the feeding grounds, as the values are relatively unchanging for both cohorts.

Northeast Coast mean salmon scale $\delta^{13}C$ values show strong, cyclical patterns that are similar through time for both cohorts, with an apparent periodicity of approximately seven years, see Fig. 4.3. The similarity in cycles shown by the $\delta^{13}C$ values of the two cohorts is maintained throughout most of the years sampled between 1985 and 2001. The between-year variances in the $\delta^{13}C$ values for these cohorts are higher than those of the corresponding River Frome cohorts, which, together with the large, cyclical patterns in annual mean $\delta^{13}C$ values through time imply that the baseline $\delta^{13}C$ values over the time covered by these analyses are highly variable in the feeding grounds. This high variability suggests that ocean climate conditions, which directly and indirectly control $\delta^{13}C$ values in marine ecosystems (see section 3.2), vary significantly and thus are likely to have implications for numbers of fish surviving to make the spawning migration home.

The two populations sampled here show remarkably contrasting results in carbon isotopes, with the River Frome salmon separated by cohorts through time, and the Northeast Coast salmon showing very similar trends and values between cohorts, indicating that the former have different feeding grounds at sea, and the latter have similar feeding grounds for both cohorts. These contrasts are maintained through time, with much greater variation seen in the $\delta^{13}C$ values, and therefore in the climatic conditions, of the feeding grounds occupied by the Northeast Coast fish, and much more stable conditions in both of the River Frome grounds. These results also show that variation in $\delta^{13}C$ values of the Northeast Coast grilse and MSW salmon is greater than in the corresponding cohorts of the River Frome salmon, see Table 3.7. The higher variations in the Northeast Coast cohorts correspond to higher levels of baseline variation, as discussed above, than seen in the Frome cohorts.

6.2. Comparison of $\delta^{15}N$ values

Salmon from the River Frome show significant separation between grilse and MSW cohorts in $\delta^{15}N$ values, as discussed in chapter 3 (see Table 3.2 for ANOVA results), with significantly elevated values in MSW fish. This relative enrichment in MSW fish ^{15}N is as expected with some level of trophic control. The positive relationships between $\delta^{15}N$ values and mass for both cohorts are further evidence that $\delta^{15}N$ values are partially controlled by trophic enrichment, but there is also likely to be a strong baseline component in the $\delta^{15}N$ values due to variation about the linear relationship. This strong baseline component is supported by the retained separation in $\delta^{15}N$ values between the cohorts after mass correction on the $\delta^{15}N$ data from both grilse and MSW fish, with the majority of the variation remaining in the data after correction, suggesting that a major control on $\delta^{15}N$ values is that of the baseline ecosystem signal. These results suggest that grilse and MSW fish from the River Frome are feeding at different trophic levels and in areas with differing baseline conditions during their final season of marine growth.

River Frome and Northeast Coast grilse have more variable $\delta^{15}N$ values than MSW fish from these populations, even after mass correction, suggesting either that they are feeding in an ecosystem with more variable baseline conditions, more variable prey species dynamics, and/or more opportunistically across a wider range of trophic levels than the MSW salmon. These results potentially indicate a dietary shift away from opportunistic and poorly constrained prey types in younger, smaller salmon towards a prey type more constrained by gape size in larger, older salmon. This apparent change in foraging strategy may indicate a change to piscivory at a certain mass, which, given that the inflection points of the logarithmic relationships between $\delta^{15}N$ values and mass in both populations is around 4-5kg, is likely the crucial mass value at which diet changes. Most fish returning as grilse appear never to make this change, whereas most MSW fish do. Thus the change in prey type may indicate a physiological or behavioural change associated with the adoption of a multi-sea winter life history strategy.

River Frome salmon scale $\delta^{15}N$ values show no significant patterns or trends through time for either cohort, see Fig. 4.7, although, as mentioned above, grilse are more variable than MSW fish (see F tests near the start of chapter 3). The separation in $\delta^{15}N$ values is maintained throughout almost every year sampled between 1971 and 2002 (see Fig. 4.7) indicating that trophic and baseline separation are also maintained through time, as might be expected for the size difference in the cohorts, and also based on the separation in $\delta^{13}C$ values discussed above.

Salmon from the Northeast Coast also show significant separation between grilse and MSW cohorts in $\delta^{15}N$ values, as discussed in chapter 3 (see Table 3.2 for ANOVA results), with significantly elevated values in MSW fish. This relative enrichment in MSW fish ^{15}N is as expected with some level of trophic control. The minimal change in $\delta^{15}N$ values post-mass correction (see Table 3.4) suggest that baseline ecosystem $\delta^{15}N$ values may control the majority of variation in salmon scale nitrogen isotope values within each cohort, although some level of trophically controlled variation would also be expected, particularly with the isotopically heavier MSW fish compared to grilse. It is not, however, currently possible to partition the nitrogen isotope variation into trophic and baseline components.

Northeast Coast salmon scale $\delta^{15}N$ values show contrasting trends through time, with a significant decline in grilse, but no observable pattern in MSW fish (see Fig. 4.12). The separation in uncorrected $\delta^{15}N$ values is maintained throughout almost every year sampled between 1985 and 2001, but this separation collapses post-mass correction (see Table 3.4), indicating that trophic separation is also maintained through time, as might be expected for the size difference in the cohorts. The difference in $\delta^{15}N$ values between the cohorts, however, is considerably smaller than in the River Frome population, despite a similar separation in sizes, indicating that the baseline conditions, which appear to control the majority of the $\delta^{15}N$ variation, are much more similar for the Northeast Coast population.

Contrary to standard isotope ecology theory where $\delta^{15}N$ values are most strongly controlled by trophic level (Ciancio et al. 2008; DeNiro & Epstein 1981; Wada et al. 1991b), these results indicate that a large proportion of the variation in the isotopic composition of nitrogen in Atlantic salmon scales for both populations is controlled by variations in ecosystem baseline $\delta^{15}N$ values, as shown in Pacific tuna (Graham et al. 2010), dab and whiting (Jennings & Warr 2003). These results also show that variation in $\delta^{15}N$ values of the Northeast Coast grilse and MSW salmon is greater than in the corresponding cohorts of the River Frome salmon (see F tests near the start of chapter 3, and in Table 3.7). The higher variations in the Northeast Coast cohorts correspond to higher levels of baseline, and potentially trophic variation, than seen in the Frome cohorts.

6.3. Mass comparison

Grilse and MSW fish for both cohorts had similar mass values on return (RF grilse 3.36kg ±0.98, NE Coast grilse 3.00kg ±0.84; RF MSW 6.39kg ±1.92, NE Coast MSW 6.28kg ±1.49) for the fish analysed isotopically. This in itself is an interesting result, as it shows that the average MSW fish is twice the mass at return of the average grilse. Returning mass might, therefore, be used as an additional independent tool to validate classification into marine age classes where the age of the fish based on scale reading is not entirely clear. It must be noted, however, that the mass values investigated here are only those taken from the fish analysed isotopically within each population, and therefore require validation using mass data from a larger proportion of each population to determine whether the observed patterns are population-wide.

Average mass values of returning River Frome grilse showed a significant temporal decline between 1971 and 2002, see Fig. 4.11, although no trends or patterns were apparent in the MSW component of the stock, or in either cohort from the Northeast Coast stock, see Fig. 4.16. These temporal analyses of mass may suggest that some factors of the marine environment have been becoming less favourable through time for growth of Frome grilse, but have not changed overall for Frome MSW salmon or for the Northeast Coast population. Overall for the Northeast Coast cohorts, it appears that factors influencing their marine growth have not changed significantly between 1985 and 2001.

6.4. Returning salmon

Numbers of salmon returning to the River Frome (direct counts of adult fish) and Northeast Coast (ICES PFA model England and Wales abundance (ICES 2008a), see section 4.4) were compared with measured isotope values and with mass for grilse and MSW fish from each population, in order to ascertain whether these factors exerted controls on numbers of returning adult fish.

Numbers of adult fish (grilse and MSW) returning to the River Frome dropped from approximately 2000 to 3000 down to around 1000 to 1500 in the 1970s, recovered briefly in the late 1980s, and then fell again to around 1000 to 1500 individuals or fewer, where they have remained since the early 1990s (see Fig. 4.21). These numbers were compared with the $\delta^{13}C$ values of grilse and MSW salmon scales for corresponding years, and lagged relationships found to exist for both cohorts from this population (see Fig. 4.24). These results were unsurprising given the stability in temporal $\delta^{13}C$ values, which indicate that climatic conditions in the feeding grounds of these cohorts are relatively stable, and therefore unlikely to influence the numbers of fish surviving to return in the short term, although climate appears to be a long term ($\geq$14 years) control on return numbers.

Numbers of adult salmon returns to England and Wales from the ICES PFA model (ICES 2008a), were used as proxies for returning numbers of grilse and MSW fish to the Northeast Coast population (see Fig. 4.22). Northeast Coast driftnet fishery catch data do not reflect true abundance, as there have been reductions in fishery effort throughout the time covered here, and an unknown portion of the salmon are likely to be of Scottish origin thus estimates of returns to local rivers in this region do not reflect true abundance. The ICES model for England and Wales was thus deemed the best proxy, based on advice from Cefas. These numbers were highest in the mid-1980s at the start of these isotopic analyses of the population at around 150,000 to 200,000 fish, and dropped to around 100,000 grilse and 75,000 MSW fish in the early 1990s, around the same time as the largest decline in the Frome population. Following on from this, the ICES grilse PFA model showed a rise to around 150,000 individuals, followed by a heavy decline to around 75,000 in 1996, from whence the numbers were relatively stable until 1999, after which there was a rise to around 100,000 fish, which was relatively stable again until the end of the time-series in 2001. The ICES MSW PFA model shows that after the mid-1980s high, there was a decline in the early 1990s to around 75,000 fish, which remained at a stable level until a drop in 1996-1997 to around 30,000, followed by a rise again to around 70,000 fish, from where the model shows relatively stable numbers until the end of the time series covered here, in 2001. Despite differences in absolute numbers between the cohorts, the overall patterns are relatively similar, see Fig. 4.22. These numbers were compared with the $\delta^{13}C$ values of grilse and MSW salmon scales from the Northeast Coast for corresponding years, and significant positive relationships were found to exist for both cohorts (see Fig. 4.25), with a return period of ≤ six years. The positive sign of these relationships indicate that conditions conducive to more positive $\delta^{13}C$ values in the Norwegian Sea are likely to be good for the return rates of Northeast Coast salmon. The more positive $\delta^{13}C$ values are likely to be linked to SST through the mechanisms discussed in previous chapters, e.g. the Climate section of chapter 1, and section 3.3 (Hofmann et al. 2000; Popp et al. 1989; Rau et al. 1996; Switzer et al. 2003; Tamelander et al. 2009; Vander Zanden & Rasmussen 1999). These relationships between numbers of returning fish and $\delta^{13}C$ values indicate that ocean climate variability in the feeding grounds of these populations and the physiology linked to it are exerting strong controls on marine mortality and return rates of the salmon analysed here.

Numbers of returning salmon for each population were then compared to the $\delta^{15}N$ values for their cohorts. In the River Frome, significant, positive lagged relationships were found between returning numbers of adult fish and $\delta^{15}N$ values of both grilse and MSW fish, both before and after correction for mass effects (see Fig. 4.26). These relationships indicate that higher numbers of returns occur three to five years before high $\delta^{15}N$ values, which suggests that the dynamics of high trophic level prey exert control over the abundance of returning salmon. A similar pattern was seen in Northeast Coast MSW salmon (Fig. 2.27), which also had a significant positive relationship between $\delta^{15}N$ values and returns with a lag of around plus five years; this pattern was not seen in grilse, however, where the significant positive lag was offset by minus one year, indicating that high returns occurred one year after high $\delta^{15}N$ values. The patterns of $\delta^{15}N$ correlation with returns in the Northeast Coast population broke down, however, when correction for mass effects was applied, likely due to the number of years for which mass data were not available, meaning that these years had to be excluded from the analyses. Differing patterns are seen in the River Frome population and Northeast Coast MSW fish, characterised by a positive lag between $\delta^{15}N$ values and returning numbers, versus the Northeast Coast grilse cohort, which is characterised by a negative lag., In the former group, baseline $\delta^{15}N$ values, controlled by factors such as nitrate availability and productivity (Lara et al. 2010; Waser et al. 2000), or prey abundance dynamics appear to exert a control on returns (Peyronnet et al. 2008), , while trophic status may be more important for returns in the latter,.

Mass values of the fish analysed from both River Frome cohorts and from Northeast Coast grilse were found to have significant relationships with annual returns, but no relationship was seem between mass and returns for Northeast Coast MSW fish (see Fig. 4.28), although this may be due to the high number of fish analysed for which no mass data were available. The correlations for the other groups suggest that the mass of the returning fish exerts a control on their success in survival and/or return migration. Interestingly for the Frome cohorts, the significant cross-correlations were negative at around year zero, suggesting that returns were higher when fish were smaller, although this might be an artefact of attempting to represent the mass of an entire population using only a few hundred samples. In the Northeast Coast grilse, however, the relationship was significant and positive at year zero, which might be predicted as larger fish might be expected to withstand the rigours of migration and fasting more successfully (Fleming 1996; Friedland 1998; Friedland et al. 2005; Friedland et al. 2000; Jonsson & Jonsson 2003b). These observations are based solely on sampled fish and ideally should be tested with larger datasets, although there are relatively few available historic records of both the mass of returning grilse and MSW fish and the total numbers of returns for these cohorts.

The results of these analyses of returns against isotope values and mass have very important implications for conservation and management within this population. In populations such as these, where the return rates are heavily influenced by ocean climate, river habitat management may not be the most effective use of resources to restore, maintain and increase salmon numbers. Alternatively, an adaptive management strategy might be more useful, where localised climatic conditions in the feeding grounds could be monitored, and this information used to set variable quotas for fisheries and angling. In populations where mass effects are important in determining return rates, monitoring the condition of fish returning to the rivers may be central to successful management. In cohorts where baseline nitrogen or trophic level effects are important, ocean colour indices of productivity, or the monitoring of prey species dynamics might be essential for management and conservation measures. The effective application of any measures aimed at predictively managing and conserving these declining populations where they are controlled by open ocean conditions, as discussed above, is dependent on some prior knowledge of the areas of sea used by each population and cohort therein.

6.5. Maps

Previous research on salmon at sea has often focussed on linking patterns in abundance to productivity (Crozier et al. 2004; Friedland et al. 1999; Quinn et al. 2006) or to large scale ocean climate indices such as the North Atlantic Oscillation (NAO) (Jonsson & Jonsson 2004b; Peyronnet et al. 2008). Analyses of wNAOI show some relationships between the Atlantic salmon populations investigated here, returns, $\delta^{13}C$ values and $\delta^{15}N$ values, but these relationships were not as strongly structured or significant as those between returns, $\delta^{13}C$ values and $\delta^{15}N$ values, suggesting that broadscale climatic factors are less influential than localised feeding ground conditions in terms of temperature, climatic variability, productivity and the dynamics of prey species, for example.

Given that there is evidence for links between ocean conditions of climate and productivity and abundance of returning salmon, as previously discussed, it is logical to assume that salmon are affected by these factors on a more local scale. SST variations across the North Atlantic were thus correlated with the $\delta^{13}C$ values of grilse and MSW salmon for each population for every individual degree of the North Atlantic between 60ºW to 20ºE and 45ºN to 75ºN. Correlations between time series of scale $\delta^{13}C$ values and SST vary spatially across the possible range for Atlantic salmon. The spatial distribution of correlation coefficients is highly structured, and provides estimates of location that are consistent with known salmon feeding grounds. Highest correlations, and thus likely feeding areas, for both the grilse and MSW components of the Northeast Coast mixed stock are found in the Norwegian Sea. Correlations for the grilse component of the Northeast Coast stock are relatively low, perhaps reflecting a greater range of feeding locations within this population, but the region of highest correlation is located north of the Faroe Islands (Figs 5.5 & 5.6). Tissue isotope records for the MSW component of the Northeast Coast stock are highly correlated with SST in the Norwegian Sea (Figs 5.7 & 5.8). These results are consistent with tag-recapture datasets (Holst et al. 1999; ICES 2008b, 2009c), and suggest that fish originating from the Northeast Coast of the UK follow the easterly branch of the North Atlantic current into the Norwegian Sea (Dadswell et al. 2010). In contrast, our results suggest that fish from the River Frome feed in more westerly regions, with returning grilse occupying an area close to the shelf break around north and east Iceland (Figs

5.1 & 5.2). The isotopic composition of MSW fish returning to the River Frome strongly implies marine feeding off Iceland (Figs 5.3 & 5.4). Tagging databases show that southern European origin fish are caught more frequently in the west Greenland than the Faroes fisheries (ICES 2009c), and limited fishing surveys suggest a salmon feeding ground east of Greenland, possibly in the Irminger Sea (Holst et al. 1999; Reddin 1988), indicating an overall westerly migration route for salmon originating from southern European rivers. Our results support this, suggesting that fish originating from the River Frome follow the western branch of the North Atlantic Drift current.

The results given by the maps are very interesting; they show that the putative feeding grounds of all four cohorts are close to nutrient-rich shelf break areas, often around the spawning or feeding grounds of preferred forage fish for Atlantic salmon (Haugland et al. 2006; Holst et al. 1998; ICES 2009a; Jacobsen & Hansen 2001).

6.6. Conclusions summary

Isotope analyses of carbon and nitrogen in the collagen of Atlantic salmon scales returning to their natal rivers may be used to obtain essential information about the ecology of the salmon's final season of marine growth. These isotopes carry information about climatic conditions, productivity and trophic structure in the feeding grounds of the salmon during the growing season, and may thus be used to find reasons for patterns of abundance in returning salmon. Based on the results of stable isotope analyses, the hypotheses set out in chapter one of this thesis have been answered as follows:

1. There is trophic separation between the smaller grilse cohort and larger MSW cohort. Accepted, see chapter 3 for details, and chapter 4 for temporal analysis.
2. Salmon from different English populations feed in a common marine area during the growth season prior to return. Rejected; both the bulk and temporal $\delta^{13}C$ signals are significantly different between the River Frome and Northeast Coast populations, see chapters 3 and 4 for details.
3. Grilse and MSW salmon from the same natal origin feed in different areas in the season prior to return. Partially accepted, but population specific. Grilse and MSW fish from the Northeast Coast do appear to share feeding grounds, as there is no significant difference between $\delta^{13}C$ values of the cohorts in this population. Both the bulk and temporal $\delta^{13}C$ signals are significantly

different between cohorts in the River Frome, however, indicating that these cohorts maintain marine segregation during their final summer season on the feeding grounds prior to return.

4. Salmon from English populations share feeding grounds with grilse from Newfoundland. Rejected, as both the $\delta^{13}C$ and $\delta^{15}N$ values are significantly different between all cohorts of the two UK populations and the Canadian grilse analysed, see chapter 3 (Table 3.7) for details.

In addition to these initial hypotheses, the patterns in temporal variation of isotopes in animal tissues are also useful in determining migration paths and the locations of feeding areas (Rubenstein & Hobson 2004). These patterns have been used here to map the likely population- and cohort-specific marine feeding grounds for grilse and MSW salmon in the North Atlantic Ocean for the first time. This research has shown that different populations and their cohorts, from a relatively small area of the natural range of the Atlantic salmon, are subject to differing controls on their abundance, and that they occupy specific, segregated feeding grounds within the marine environment. Moreover, it appears that the salmon from these populations return year-on-year to their cohort-specific feeding grounds, providing, therefore, targeted areas for monitoring, management and conservation of these dwindling stocks.

6.7. Future work

The research discussed here has, to date, been applied to two separate Atlantic salmon populations within the UK. Future research on the Atlantic salmon will focus on expanding the populations analysed to include most of the British Isles, with potential for investigating populations across the species range, from Finland to Spain, and across the Atlantic to Canadian and North American populations. There is also the potential for validation of the feeding grounds posited from the maps using the genetic data from the SALSEA (Salmon at Sea) project when they are published in 2011. Future work will also be carried out on the SAHFOS Continuous Plankton Recorder plankton samples to attempt to characterise baseline plankton isotope values under differing conditions and thereby test the hypotheses supplied by the maps. Further climate indices, including the Atlantic Meridional Oscillation and the El Niño/La Niña cycles will also be analysed to investigate potential effects on the salmon isotope and returns data.

The type of indirect analysis of location used here has the potential to be applied to many migratory marine species that are otherwise challenging to study directly.

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