Factors leading to variation of spawning time in the Barents Sea capelin (*Mallotus villosus*)

Samina Shirajee

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Department of Biology
University of Bergen, Norway

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SUMMARY

Barents Sea capelin (*Mallotus villosus*) is a semalparous fish species, and the timing of spawning both in terms of age and season is variable. The main spawning occurs off the northern Norwegian coast in spring, but it is also observed to spawn in summer up to three months later, and there is limited knowledge to explain why this is happening. The present thesis explores potential factors leading to variation in timing of spawning in this key species of the Barents Sea; hereunder whether seasonal timing of spawning to spring or summer is due to an established strategy and genetically (parentally) determined, or simply a variable phenomenon related to changes in environmental conditions. Comparisons of biological characteristics made between spring spawners (collected at the spawning grounds in February-March) and summer spawners (collected at the spawning grounds in June) in five selected years (1977, 1982, 1984, 1985, and 1996) demonstrated that summer spawners were significantly younger, smaller (lower length and weight), with a slower somatic growth and lower condition than spring spawning capelin. In addition, both the first year otolith growth and the ratio between first and second year otolith growth was lower in summer- than in spring spawners. First year otolith growth increased with body length at age, whereas such a relationship was not found with the ratio between first and second year otolith growth. Hypothetically capelin hatched in summer would on average have both a lower first year otolith growth and a lower ratio between first and second year otolith growth than capelin hatching in spring due to a much shorter feeding season in their first year of life. Hence, the observed differences in biological characteristics could be interpreted as capelin returning to spawn in the same season they hatched themselves as parentally determined, i.e. summer spawning is an established strategy. This was further explored using data from the late feeding distribution in the Barents Sea during August-October 1976-2012, which demonstrated that capelin with otolith growth characteristics similar to that observed among summer spawners tended to distribute more to the southeast. Feeding and growth conditions normally tend to be worse when moving towards south east, which may explain the slower growth and condition observed among summer spawners. However, the lower condition in summer could also be linked to the longer period spent from the last main feeding season in autumn until the spawning. Over the period 1976-2012 the first year otolith growth and the ratio between first and second year otolith growth were highly variable, and the fluctuations in these parameters were significantly related to population density (capelin biomass), zooplankton availability and temperature. This signifies that age at spawning, and timing of spawning within an established spawning season may vary with climatic changes and stock fluctuations. It is the conclusion of this thesis that it is not very likely that the climate may cause capelin hatched in spring to spawn in summer. However, one cannot exclude that proportions of capelin spawning in summer may vary with changes in environmental conditions, as the climate effect on recruitment may differ between spawning seasons.

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1 INTRODUCTION

1.1 Background

Importance of capelin in ecosystem

Capelin (*Mallotus villosus)* is a pelagic fish and plays an important role in Norwegian fisheries. Capelin in the Barents Sea represents the world's largest capelin stock (Gjøsæter, 1995). In some years, capelin biomass is very high and it is found to range between 6-8 million tons (Gjøsæter, 1998) which indicates a high reproductive potential and an intrinsic population growth rate of capelin (Barbaro *et al.,* 2009; Rose, 2005).

In the Barents Sea, capelin is known as the largest pelagic fish stock. In regards to energy conversion from zooplankton production to higher trophic levels, they play a significant role as an intermediary (Gjøsæter, 1998). Thus, capelin lies at the centre of food web (Bakun, 2006) and provides important linkages for energy transfer among trophic levels (Lavigne, 1996). Cod is the main predator of capelin and large numbers of capelin are consumed by cod during the spawning period. From 1984 to 2007, annually 0.2 to 3.0 million tons of capelin were preyed on by cod (Gjøsæter *et al.,* 2011). In addition, young herring is another main predator of capelin larvae (Huse and Toresen, 1995). In 1984-1986 and 1993-1994, there were collapses in the capelin stock due to recruitment failure, which was linked to the presence of large year classes of young herring (Gjøsæter and Bogstad, 1998). Capelin is also preyed upon by haddock and it happens during capelin's spawning period. Capelin is also preyed by mammals such as seals (mainly harp seals) and whales (primarily minke and humpback whales). Harp seals also eat large amount of capelin and this amount is 23 to 812 thousand tons a year (ICES, 2000). Seabirds are also predators of capelin. Guillemots and puffins are known as main avian predators.

Biology of capelin

Life history characteristics

Capelin is a small fish and it becomes maximum 22 cm long at a weight of approximately 50g (Prokhorov, 1968). Life span of capelin is very short. Capelin may live up to seven years but at present, most of the capelin is found not to exceed five years of age (Gjøsæter *et al*., 2011).

Capelin is known as planktivorous fish in the Barents Sea and copepods, euphausids, hyperiids, molluscs, chaetognats are the main food for capelin. July to October is considered the main feeding season for capelin (Gjøsæter, 1998).

Sexual maturation appears in capelin when the fish is approximately 14 cm long (Gjøsæter *et al.*, 2011). However, sexual maturation depends on other factors like growth pattern, age, sex. Maturity appears in male at relatively larger size than female (Gjøsæter, 1998). Depending on the growth, capelin spawns at the age of 3-5 years (Gjøsæter *et al.*, 2011) .Capelin spawns typically only once during their life time (i.e. semelparous) and after spawning most of the capelin are not able to survive (Christiansen *et al.*, 2008).

Distribution and migration

Generally, capelin stays in the Barents Sea from the larval stage until death and extensively migrates to different areas of the Barents Sea for feeding and spawning purposes. However, in which areas capelin will be distributed for spawning, feeding and nursery purposes depend on hydrographic conditions (Gjøsæter and Loeng, 1987). Usually capelin migrates toward the north and the north-eastward for feeding purposes during summer and autumn (Gjøsæter, 1998), and during the winter and early spring the capelin that has reached maturity migrates towards the northern part of the Norwegian coast (Troms and Finnmark counties) and Russia (Kola county) for spawning activities. However, this migration pattern could be changed due to the fluctuation in temperature in the Barents Sea (Gjøsæter, 1998). In addition, most of the time capelin uses two or three different migratory routes to reach the coast (Gjøsæter, 1998); in warm years most of the mature capelin migrates from the north-east Barents Sea to the coast of Finnmark and the Kola peninsula, whereas in cold years they may migrate from the south of Bear Island to the west coast of Troms and Finnmark.

Spawning time and spawning area of capelin

There are two modes of reproductive behaviour in capelin. One is known as beach spawning which mostly occurs in the Pacific and Newfoundland regions whereas deeper water spawning, another form of reproductive mode in capelin, is dominant in Icelandic and Norwegian waters (Rose, 2005). Timing of spawning is a very important factor in the life cycle of the fish. Main spawning period for capelin is March–April and spawning is observed in Norwegian coast and

Russia from about longitudes 15-37°East (Figure 1), but in some years capelin is also observed to spawn during summer (Gjøsæter *et al.*, 2011). Spawning is not observed each year at the entire range of longitudes 15-37°; spawning may vary between the western, central and eastern spawning areas. Spawning timing and area may also depend on the coastal water's temperature (Gjøsæter *et al.*, 2011). Optimum water temperature for spawning grounds at the Russian coast is 2-4°C and in northern Norway is 4-6°C (Gjøsæter *et al.*, 2011). For example, when capelin migrates to the western spawning grounds temperature has been observed to be above normal. In 1997 spring-spawning took place in the eastern Murman coast, but in the same year some capelin also spawned in mid-August and the spawning area expended into the western part of the Kara Sea due to the fact of slower maturation. Fat accumulation was low year prior to spawning which causes slower maturation (Gjøsæter *et al.*, 2011).
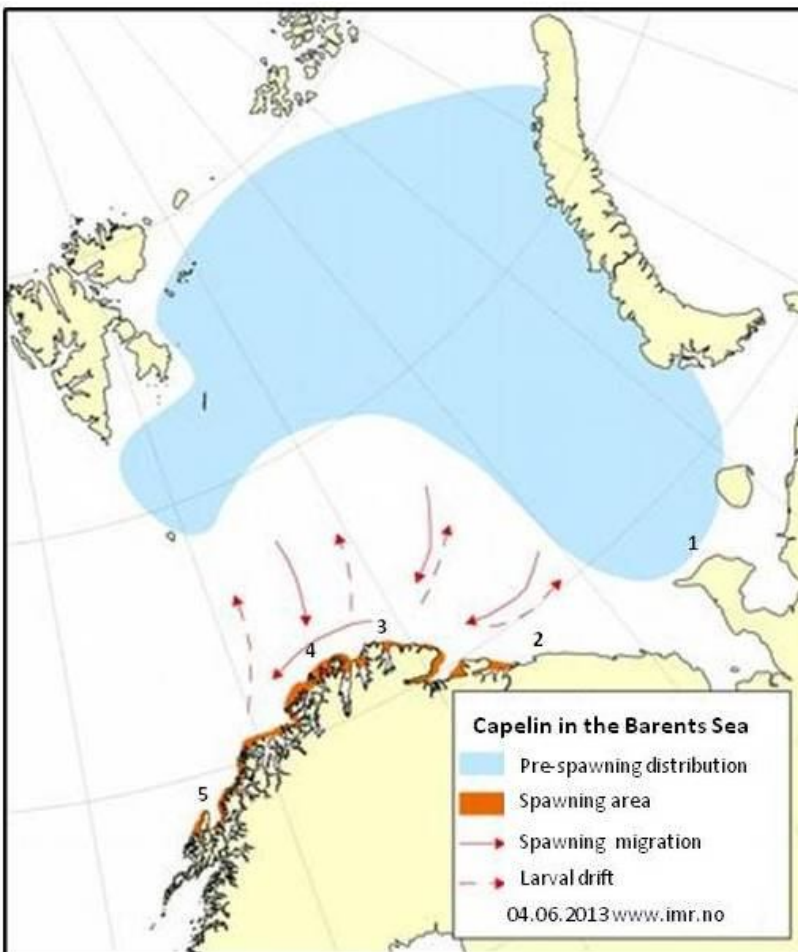
Figure 1: Spawning ground (Areas 1-5) of capelin in the Barents Sea (Source: Adopted from Institute of Marine Research, http://www.imr.no/temasider/fisk/lodde/lodde/nb-no).

General plasticity in spawning time in fish

It is not only capelin that has plasticity in spawning time, this is common in fish (Karino and Kuwamura, 1997; Olsen *et al.*, 2010). Spawning time of the temperate fish species is generally believed to have evolve due to the fact that with changes in environmental conditions, which play an important role for early stages of life in fish and their survival (Cushing, 1969).

Biological parameters such as size and age are linked to maturation and spawning time in fish (Hutchings and Myers, 1993). Moreover, in general lifetime reproductive success of animals depends on these two parameters (Stearns, 1992; Bernardo, 1993). Furthermore, maturity changes are linked to two non-exclusive hypotheses including (Browman, 2000; Law, 2000; Heino and Godø, 2000; Heino *et al.*, 2002).

1. 'Compensatory response' hypothesis which predicts that if fish grow very fast, maturation will appear early in life. This early maturity happens due to reduced stock size. This reduced stock size leads to less competition for the resources, which is responsible for compensatory growth; and

2. 'Evolutionary response' hypothesis that predicts that maturity in early life is also influenced by genetic factors. Thus, genetic changes in some characteristics are responsible for maturation

Variation in the timing of spawning may be linked to age, size, condition and other factors such as geographic distribution, climatic conditions, and nutritional status of fish (Rajasilta, 1992; Slotte, 1999; Weiland *et al.*, 2000). Weiland *et al.* (2000) found that during the 1970s and late 1980s the highest number of cod spawned during the end of April to mid-June with a significant shift in the 1990s when spawning period moved to the end of July. Water temperature, population density and availability of food were the key factors that contributed to the variation of timing of spawning in cod in Bornholm Basin of the Baltic Sea. Moreover, it was evident from Marteinsdóttir and Björnsson (1999) that during 1994-1997, compared to the smaller and younger female cod, larger and older ones spawned earlier and over an extended period of time in the southwest of Iceland. In contrast, during the period of 1998-1999 larger and older female

cod spawned later instead of earlier. A number of factors including biological, physiological and behavioural condition were identified as responsible for late spawning in this category of cod (Marteinsdottir and Björnsson, 1999).

Lack of knowledge on plasticity of spawning time in capelin

It is important to understand variability in spawning time in the Barents Sea capelin. Not only variability within a spawning season, but also why some chooses to spawn in another season. Very little is actually known about the summer spawners in the Barents Sea capelin. In general changes in environmental conditions could potentially explain the occurrence of such late spawners. Initiation of feeding, maturation, and migration are closely correlated and may be all these factors are influenced by temperature (Shackell *et al.*, 1994) and may affect maturation and timing of spawning (Carscadden *et al.*, 1997). Accordingly, if zooplankton production is late during the cold year, as well as feeding, maturation, and migration, it may lead to late spawning (Carscadden *et al.*, 1997).

However, the timing of spawning in capelin, especially the occurrence of both spring and summer spawners within the same year, may also simply be based on a well established strategy. Within a species, there may be different populations spawning at different times of the year, for example, herring populations spawn typically either in the spring, summer, autumn or winter (Haegele and Schweigert, 1985). This means that a population will continue to spawn at the season as they were hatched themselves. This could be due to parental or genetic effect and not the external factors. Such an established strategy may lead to very different growth patterns, as observed in herring otoliths, to an extent that it is possible to identify individual fish to a spawning population (Brophy *et al.*, 2006). The basis for using otoliths in a similar way to study differences between spring and summer spawning capelin is clearly there, since IMR (Institute of Marine Research) has measured the width of annual increments in capelin otoliths since the 1970s.

It is pertinent to see where the summer spawning capelin are distributed in the years prior to spawning since one may question whether they have a similar distribution as the main stock spawning earlier in spring. One may question whether it is a difference or change in feeding

distribution that causes some capelin to spawn in summer instead of spring. Larval drift patterns may clearly differ between early spring period and summer period as wind and current systems differ (Bjørke *et al.,* 1986) which may lead to different larval drift routes, nursery areas etc. Moreover, IMR has a long time data series on capelin abundance and distribution during the autumn in the Barents Sea, and given the above mentioned potential differences in growth and otolith characteristics between spring and summer spawners, it may be possible to examine the differences in distribution between the two spawning groups.

The potential differences in distribution of spring and summer spawning capelin may also be variable and linked to interannual changes in larval drift related to changes in weather and currents (Vikebø *et al*., 2007). Changes in environmental conditions may also result in differences in recruitment between the two spawning groups, as it has been observed in herring spawning in same area at different times of the year (Husebø *et al*., 2005). Variations in somatic and otolith growth of young herring in fjord nursery areas have also been linked to fish density and temperature (Husebø *et al*., 2007). Similar effects on recruitment and growth related to stock size and environmental conditions could be expected on capelin, leading to potential variations in autumn distribution of spring and summer spawning capelin.

1.2 Objectives of the thesis

Based on the background information above, the main objective of the present thesis is to explore the potential factors leading to variation of spawning time of the Barents Sea capelin; such as effects of somatic growth, age of maturation, body condition (weight at length), geographical distribution and climatic conditions. Hereunder, to explore whether seasonal timing of spawning to spring or summer is due to an established strategy and genetically (parentally) determined, or simply a variable phenomenon related to changes in environmental conditions.

2 MATERIALS AND METHODS

2.1 Biological samples

Data on capelin collected by IMR were used to analyse the biological factors leading to variation in spawning time of the Barents Sea capelin. These data was based on annual surveys in the Barents Sea winter survey, 0-group survey, capelin survey, spring survey (limited years) and autumn survey, besides data from samples from commercial fishery. This thesis used the data for the period of 1976 to 2012. Various kinds of fishing methods like, pelagic trawls, gill nets, seine fishing were used to collect the samples. Different pelagic trawls for example, 'Harstad-trawl' and 'Åkra-trawl' were used to collect capelin. Usually, it is easy to catch capelin using 'Åkra-trawl' yet, 'Harstad-trawl' is also extensively used to collect the capelin. To furnish these two types of trawl, small mesh (4mm) net was used (Gjøsæter, 1999). In this thesis all gears are used based on the assumption that the analyses carried out are not influenced by sampling gear.

2.2 Biological data

Different types of biological parameters such as total length, weight, age, sex, maturity stage have been measured for individual fish and have been analysed in the present thesis. Here, length, weight and age from otolith were measured by IMR's experienced readers. Sex and maturity stages were also identified by the staff of IMR. All capelin have been classified into eight maturity stages after the visual inspection of gonads. Of these stages, stage 1-2 known as immature stages, 3-5 maturing or pre-spawning stages, stage 6 spawning, stages 7 and 8 respectively known as spent and resting stage (Mjanger *et al*., 2006). The stages were important for the selection of data used in the analyses.

Age and growth determination by using otoliths

An important basis to identify the potential effects of somatic growth on the timing of spawning in capelin was the increments in capelin otoliths. The number of winter increments indicate the age of capelin. As for other fish in the northern hemisphere, all capelin by convention shift their age on January 1st. However, to detect accurate life span by age is difficult. According to Gjøsæter (1999) the measurement of winter ring is essential for both purposes such as growth

study and age identification. Three pairs of otoliths are available and these are sagittae, lapilli, and asterisci. Saccular otoliths—the sagittae, are important in management of capelin because these are the most commonly used otoliths for studying age (Gjøsæter, 1999). For capelin otolith analyses, 40X magnification is most often used (Mjanger *et al*., 2006). In the otolith analyses, the radius is measured through a line from the centre to the edge of the otolith at a right angle to the rostrum and growth increments are marked as annotations at respective annuli (Figure 2).
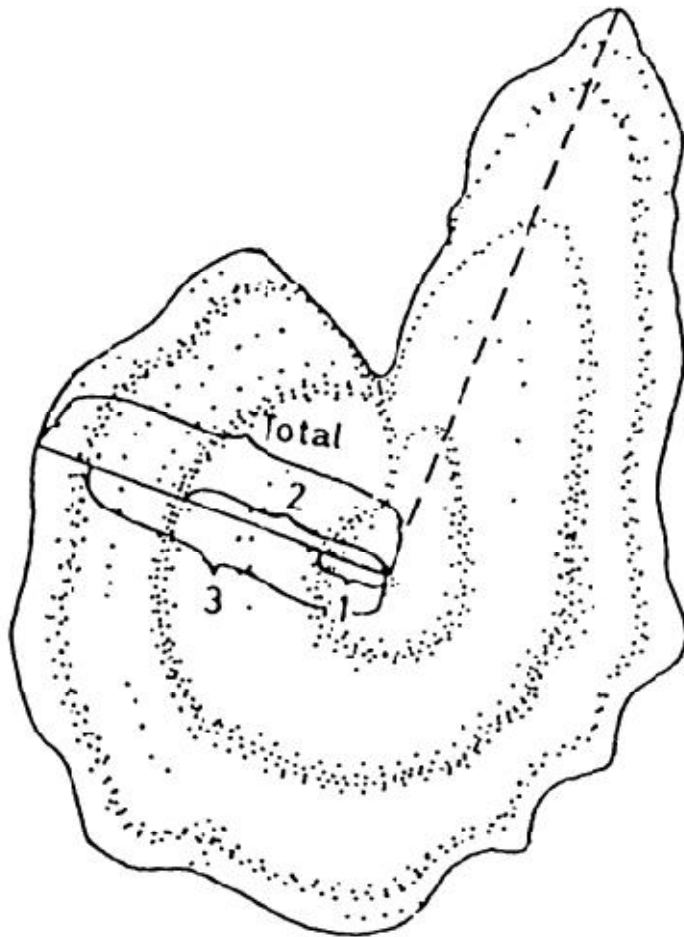
Figure 2: Capelin otolith with annotations at respective annuli and outer edge (adopted from Mjanger *et al*., 2006).

The data used in this thesis is based on the measurements of the annual otolith growth increments of more than 380.000 individuals. Annual otolith increment growth was routinely measured by experienced readers of IMR. Two measurements were used in the present study:

a. Vs1mm (1st annuli): 1st year increment size
b. Vs2mm (2nd annuli): 2nd year increment size

Length-otolith relation

The size of otolith usually represents the size of fish (Campana and Neilson, 1985). Here, for example, in 1977, total otolith increment (vstotmm) has a positive linear relationship with total size of capelin (Figure 3). Therefore, in this study otolith increment has been used as a proxy of size of capelin.
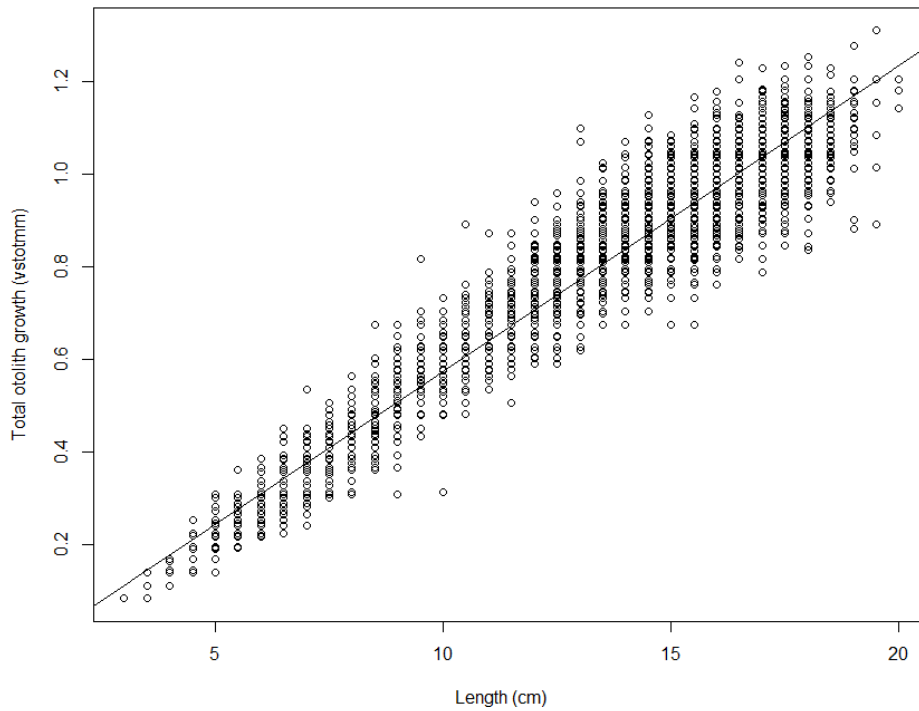
Figure 3: Relationship between total otolith increment (vstotmm) and total length (cm) of capelin in 1977.

Use of vs1mm and the ratio (vs1mm/vs2mm)

It was hypothesised that measures of growth increments in the otolith could be used to indicate a potential parental effect, i.e. spawning occurs in the same season as the capelin hatched themselves. Both vs1mm and the ratio (vs1mm/vs2mm) were used for this purpose, which is based on some underlying assumptions. It was assumed that the vs1mm typically would be lower for a capelin hatched in summer than in spring, due to a shorter feeding season. Hence, observed differences in vs1mm in capelin samples could be used as an indication of different fractions of spring and summer spawners. However, vs1mm was also assumed to be tightly linked to changes in climate and food conditions, i.e. a low vs1mm could simply be a result of a period with reduced growth related to temperature and zooplankton availability. Therefore, the ratio (vs1mm/vs2mm) was also analysed, as this was expected to be less influenced by climate change, i.e. the ratio would be expected lower for individuals hatched in summer than spring regardless of growth conditions experienced over the two feeding seasons.

2.3 Study area

The Barents Sea is a shallow continental shelf area and the average depth is 230m. It is also known as high latitude area. The northern side is bounded by the archipelagos of Spitsbergen and Franz Josef Land. The eastern and southern side is bounded by Novaya Zemlya and the northern Norwegian and Russian coasts respectively (Gjøsæter, 1998; Sakshaug and Kovacs, 2009).

The Norwegian Coastal Current is running across the Norwegian and Russian coasts (Figure 4). This current is named as Murman Coastal Current when it crosses the boarders of these two countries. From the south west side, the Norwegian Atlantic Current runs through the Barents Sea and it creates two flowing branches, one is eastwards and other is north-eastwards.
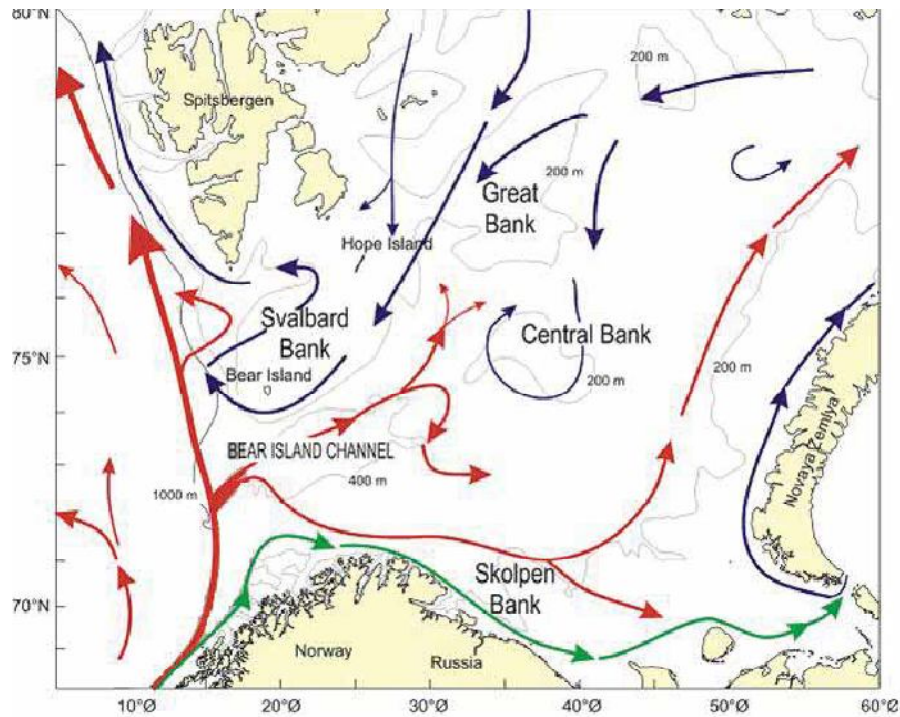
Figure 4: Map of the Barents Sea and the system of the predominate currents. Red (Atlantic waters) and green (coastal waters) indicate warm currents, and dark blue indicates cold currents (Drevetnyak *et al*., 2011).

In the Barents Sea, there are three main types of water masses; coastal water, Atlantic water, and Arctic water (Gjøsæter, 1998). Among these water masses, the inflowing amount and properties of Atlantic water masses are important for the Barents Sea because they are the determining factor for climate of the Barents Sea (Loeng, 1991; Loeng *et al*., 1997).

2.4 Selection of data for statistical analyses

The following variables/parameters were used in the analyses of biological factors on spawning time: year, month, position, statistical area, length, weight, sex, maturation stage, age, vs1mm, vs1mm/vs2mm. Environmental data selected to represent climatic factors were temperature and zooplankton (see further down in page 18 and 19). In addition, data on capelin acoustic abundance (see further down in page 18 and 19) were used for analyses of density effects. For the purpose of the study, I selected sub-sets of the data, and in the following I will explain why I selected these sub-sets.

Year

A main basis for analysing factors that affect the timing of spawning in capelin would be a thorough comparison of biological characteristics between fish spawning in spring and summer. Only a few years with the occurrence of fish in both spring (February and March) and summer (June) spawning periods were available for such comparative analyses (see Table1, Appendix 1 and Figures 5-6). It is evident from the Table 1 that most of the fish (summer spawners) were found in the selected five years (i.e. 1977, 1982, 1984, 1985, and 1996). Moreover, it is also evident from Figures 5-6 that in the selected years the fish were found near the coast. These factors lead me to select the selected years for the purpose of my analysis.

Table 1: Number of fish in spring and summer spawning period in selective years. Mature, spawning and spent stages fish and statistical areas 1-5 (Norwegian/Russian coast) were used.

Period	Year	Age 2			Age 3			Age 4			Age 5			Grand total
		Female	Male	Total	Female	Male	Total	Female	Male	Total	Female	Male	Total	
Spring	1977	0	0	0	35	16	51	318	239	557	165	154	319	927
	1982	0	0	0	7	14	21	28	32	60	4	11	15	96
	1984	2	1	3	547	376	923	1485	1396	2881	60	160	220	4027
	1985	14	25	39	196	214	410	340	457	797	11	38	49	1295
	1996	22	5	27	59	72	131	27	57	84	2	0	2	244
Summer	1977	0	0	0	43	9	52	77	23	100	47	13	60	212
	1982	50	28	78	80	28	108	33	20	53	4	1	5	244
	1984	23	2	25	390	110	500	78	104	182	0	2	2	709
	1985	2	13	15	40	25	65	6	31	37	1	6	7	124
	1996	409	187	596	108	49	157	26	10	36	4	0	4	793

However, for the analyses of potential effects of distribution, climate and population density on spawning time, the available capelin data from the years 1976-2012 (Table 2) were selected, as here the focus was the total population in years prior to spawning.
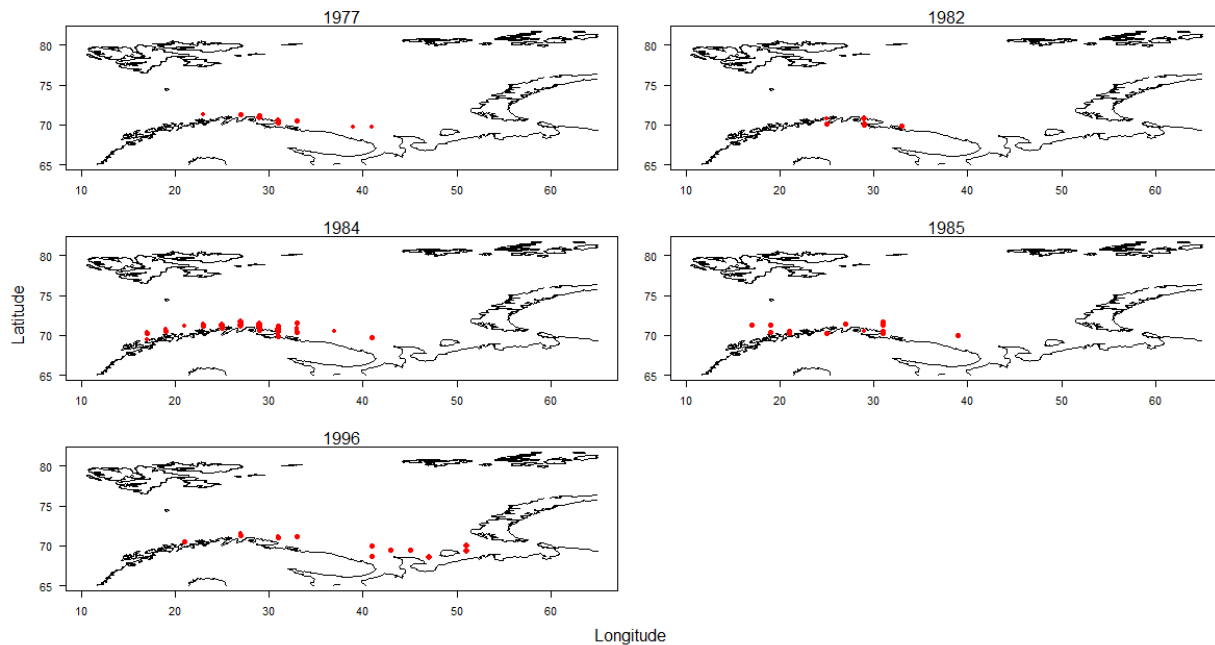
Figure 5: Annual geographical distribution of biological samples of mature, spawning and spent stages used when comparing biological characteristics between fish spawning in spring and summer (both seasons merged) in sampling years 1977, 1982, 1984, 1985, and 1996.

Stages

Mature, spawning and spent stages (3-7) of capelin were selected for comparative analyses of biological data between spring and summer spawners. The wide range of stages included was to assure a large number of fish in the analyses, and it was still assumed that the fish selected were representative of the spawning season sampled, either spring or summer. First, it was assumed that capelin in maturing stages arriving at the spawning areas in spring would spawn in spring, and not wait until summer. Similarly, spent fish in stage 7 was assumed to recently have spawned, since capelin is expected to have close to 100% mortality shortly after spawning (Christiansen *et al.,* 2008). For analyses of potential effects of distribution, the total material of capelin of all stages was included.

Statistical areas

Data from statistical fishery areas 1-5 (Norwegian Directorate of Fisheries) along the Norwegian/Russian coast were selected for comparative analyses of biological data between spring and summer spawners (Figure 6). These areas correspond to spawning areas for capelin, and it is evident from Figures 5-6 that samples and proportions of capelin in analyses representative of summer spawners were more easterly distributed. For analyses of potential effects of distribution, all areas where capelin was sampled prior to spawning during autumn surveys in the Barents Sea were included.
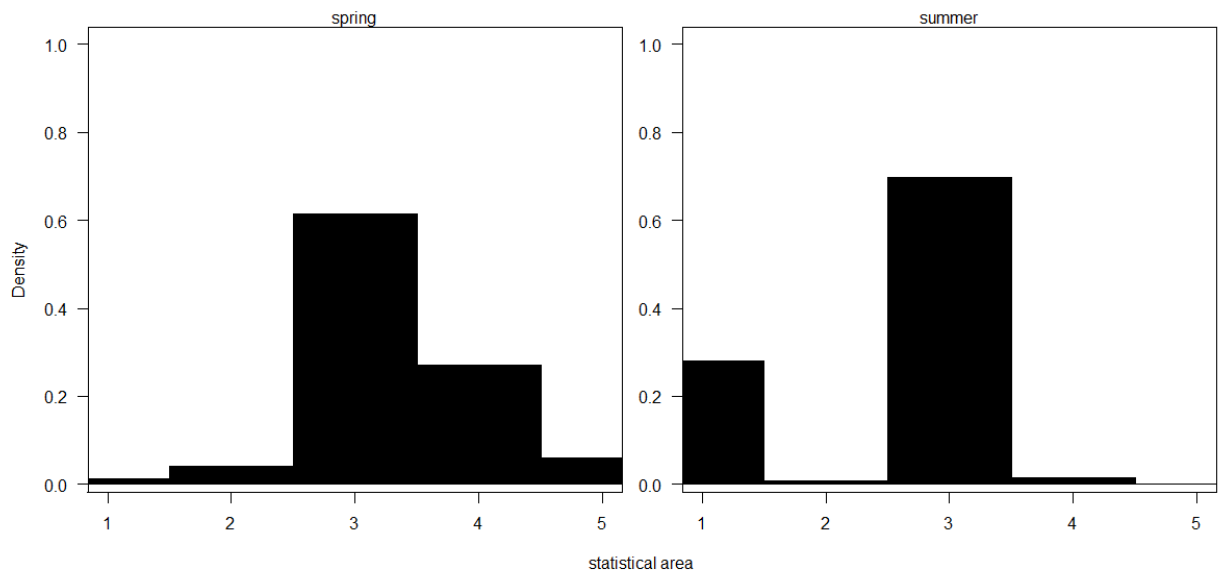
Figure 6: Proportion of capelin analysed within statistical areas 1-5 (Figure 1) when comparing biological characteristics between fish spawning in spring and summer. Data from sampling years 1977, 1982, 1984, 1985, and 1996 are merged.

Ages

In this study, only mature fish of 2-5 years old capelin were selected for analyses related to comparative analyses of biological data between spring and summer spawners, because the focus here was only the spawning population. The highest numbers of capelin were found in the two age-classes 3 and 4 (see Table 1). Yet, a large number of capelin is also available in the age

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groups 2 and 5. For analyses of potential effects of distribution, 1-5-years old capelin was selected. Again, to test the interannual differences of vs1mm and vs1mm/vs2mm 1-3-years old capelin was selected while 4 and 5 years old capelin were excluded due to low number (see Table 2).

Months

February, March and June were selected for the purpose of comparative analyses of biological data between spring and summer spawners, as capelin usually spawn in spring or alternatively in summer (Gjøsæter *et al*., 2011). So, these three months have been selected to compare biological difference between early (spring) and late (summer) spawners (Table 1). April and May were excluded due to low number of capelin in these months, and it has not been observed as a spawning period for the Barents Sea capelin (Gjøsæter, 1998). For the purpose of the analysis, February and March were combined under spring period while June was categorized as summer.

August-October was selected for analyses of potential effects of geographical distribution of fish in the Barents Sea (see Table 2).

Table 2: Number of male and female capelin collected in each age group over the study period 1976-2012 (August, September and October).

Year	Age 1 Female	Male	Total	Age 2 Female	Male	Total	Age 3 Female	Male	Total	Age 4 Female	Male	Total	Age 5 Female	Male	Total
1976	1	23	24	730	831	1561	695	629	1324	356	298	654	58	58	116
1977	1	5	6	868	832	1700	718	625	1343	245	263	508	36	53	89
1978	0	0	0	426	533	959	365	322	687	43	59	102	3	7	10
1979	0	2	2	351	489	840	421	357	778	19	31	50	0	1	1
1980	639	826	1465	1107	1225	2332	1357	1228	2585	262	289	551	4	5	9
1981	366	595	961	2887	2924	5811	956	768	1724	202	227	429	4	9	13
1982	195	410	605	1668	1960	3628	879	828	1707	57	44	101	0	5	5
1983	527	1104	1631	1838	2037	3875	434	433	867	24	15	39	0	0	0
1984	313	577	890	1690	1903	3593	860	944	1804	37	75	112	0	1	1
1985	391	594	985	2259	2423	4682	2402	2101	4503	125	128	253	1	4	5
1986	222	338	560	628	845	1473	265	391	656	16	36	52	0	0	0
1987	256	359	615	305	462	767	19	10	29	1	1	2	0	0	0
1988	289	364	653	1013	1126	2139	12	10	22	0	0	0	0	0	0
1989	655	830	1485	382	457	839	139	109	248	1	0	0	0	0	0
1990	899	1279	2178	708	863	1571	161	156	317	11	10	21	0	0	0
1991	866	1269	2135	2421	2416	4837	248	269	517	4	9	13	0	0	0
1992	691	927	1618	1109	1238	2347	913	899	1812	3	10	13	0	0	0
1993	97	120	217	1093	1135	2228	412	351	763	52	61	113	0	1	1
1994	614	770	1384	252	264	516	376	444	820	10	17	27	0	0	0

Year															
1995	353	500	853	412	480	892	113	8	121	10	1	11	1	0	1
1996	493	650	1143	350	359	709	26	7	33	0	0	0	1	0	1
1997	687	830	1517	799	913	1712	44	27	71	1	0	0	0	0	0
1998	830	1149	1979	1209	1203	2412	231	151	382	7	5	12	1	0	1
1999	956	1364	2320	1409	1609	3018	440	410	850	19	14	33	0	0	0
2000	1929	2065	3994	873	801	1674	238	164	402	7	7	14	0	0	0
2001	1018	1108	2126	1956	1994	3950	285	340	625	9	5	14	0	0	0
2002	347	438	785	1084	1335	2419	787	803	1590	5	17	22	0	0	0
2003	73	102	175	348	414	762	480	622	1102	66	126	192	0	0	0
2004	659	876	1535	578	637	1215	291	360	651	35	38	73	3	0	3
2005	259	339	598	1112	1361	2473	285	192	477	28	15	43	5	1	6
2006	488	699	1187	804	922	1726	431	389	820	17	7	24	1	1	2
2007	883	990	1873	1086	1135	2221	208	230	438	17	6	23	0	0	0
2008	383	433	816	1316	1300	2616	240	278	518	6	6	12	1	0	1
2009	347	457	804	1117	1271	2388	433	578	1011	4	11	15	0	0	0
2010	465	599	1064	846	841	1687	831	927	1758	30	30	60	0	0	0
2011	268	266	534	1010	1033	2043	534	619	1153	38	86	124	1	3	4
2012	770	724	1494	513	671	1184	533	646	1179	17	32	49	0	0	0
Grand Total	18245	23981	42226	38557	42242	80799	18062	17625	35687	1784	1979	3763	120	149	269

Longitude and latitude

Longitude values greater than 10 degrees were chosen in the study as our main location of analysis i.e. the Barents Sea. For the analyses of geographical differences in vs1mm and vs1mm/vs2mm, the Barents Sea was split in three different ways. Firstly, the data was split into bins of 1 degree on the latitudinal range and 2 degrees on the longitudinal range and mean values over the whole time series were used for GIS mapping. Secondly, the Barents Sea was split into a northern (north of 75°N) and southern area (south of 75°N), to test for the effect of longitude. Thirdly, in addition to the latitudinal split, the Barents Sea was split at 35°E into north west (NW), north east (NE), south west (SW) and south east (SE) areas to study historical changes in vs1mm and vs1mm/vs2mm.

Temperature data

In order to explain potential interannual differences in vs1mm and vs1mm/vs2mm within geographical areas, the effects of three parameters (temperature, zooplankton and capelin biomass data) were tested. Temperature data collected from the Kola section. These are available from 1900-2014, but for this study I used temperature data from 1976-2012. Mean annual temperature from this region (depth interval between 0 and 200 m) was used for this analysis (Ingvaldsen *et al*., 2003; Bogstad *et al*., 2013). Kola section's temperature stands for the Atlantic domain of the Barents Sea and is commonly used as a proxy for climate change in the Barents Sea (Ingvaldsen *et al*., 2003).

Zooplankton data

The second parameter used for the explanation of interannual variation in vs1mm and vs1mm/vs2mm within geographical areas was zooplankton data available from 1984-2012. IMR collected zooplankton data from the NW and SW section of the Barents Sea during this period. Three mesh sizes ($>2000\mu m$, $1000-2000\mu m$ and $180-1000\mu m$) were used to collect zooplankton during this time. But in this study, total biomass of all size groups (dry weight gm-2) of zooplankton was used.

Capelin biomass data

The third parameter used to test for explanation to interannual variation in vs1mm and vs1mm/vs2mm within geographical areas was the total biomass of capelin in the Barents Sea (ICES, 2011).

2.5 Data analyses and statistical tests

All statistical analysis and plotting were done by using statistical programme R (R Development Core Team, 2006). All of the statistical tests assumed a significance level of 0.05.

In capelin there are sexual differences in strategies related to growth and reproductive effort (Gjøsæter, 1999), which means that analyses, figures and statistics should split by sex and test for the effect of sex.

Testing for the differences in mean size (length and weight) between spawning periods for female and male, analysis of variance (ANOVA) models of length and weight were run with spawning periods and sampling year as factors.

Non-parametric test like Kruskal-Wallis tests were used to test for differences in age composition between spawning periods for females and males on combined data for all years, as age is not normally distributed.

When testing for the differences in somatic growth in terms of mean length at age between spawning periods for female and male capelin, analysis of variance (ANOVA) models of length were run with spawning periods, sampling year and age. Here, 3 and 4 years old fish were selected for detailed testing of differences in length between spawning periods due to the fact that ages 2 and 5 has few data points.

When testing for the differences in otolith growth (vs1mm and vs1mm/vs2mm) between spawning periods, analysis of covariance (ANCOVA) models of otolith growth were run with spawning periods, sampling year and age.

When testing the effects of fish size (length) on vs1mm and vs1mm/vs2mm, analysis of covariance (ANCOVA) were run with length, spawning periods and sex as covariates. Here, 3 and 4 years old fish were selected for testing the effects of fish size on vs1mm and vs1mm/vs2mm due to the fact that ages 2 and 5 have few data points.

In addition, when testing the effects of fish size (length) on otolith growth variables (vs1mm, vs1mm/vs2mm) between spring and summer spawners of same sex, age and length, a generalized linear model (GLM) were run for year 1984 with spawning periods, age, length and sex. Here, year 1984 was selected testing the effects of fish size (length) on growth variables (vs1mm, vs1mm/vs2mm) due to the fact that other years (1977, 1982, 1985 and 1996) have less data points compare to year 1984.

When testing for differences in condition (weight-at-length) between spring and summer spawners, a generalized linear model (GLM) of weight were run with length, spawning periods, sex, year as covariates.

For analysis of potential effects of distribution, GIS mapping was used to demonstrate overall years pooled geographical differences in vs1mm and vs1mm/vs2mm from ages 1-5 years. Also the overall years pooled effects of longitude on vs1mm and vs1mm/vs2mm were run with analysis of covariance (ANCOVA) using age and area (south ≤75° and north>75°) as covariates.

To test in which areas vs1mm and vs1mm/vs2mm was higher, t-test was run between vs1mm and vs1mm/vs2mm with area (south ≤75° and north>75°)

To test whether there were interannual differences of vs1mm and vs1mm/vs2m in different regions of the Barents Sea, the effects of year on vs1mm and vs1mm/vs2mm were run with analysis of variance (ANOVA) using age, sex and area (NW, NE, SW, SE) as factors. Interannual data on vs1mm and vs1mm/vs2mm were also related to potential explanatory parameters; hereunder temperature, capelin biomass and zooplankton using analysis of variance (ANOVA) models run with additional variables area, sex and age. In this model, year counted from 1984 because zooplankton data available from 1984. For graphic illustrations of interannual fluctuations in vs1mm and the ratio vs1mm/vs2mm compared with fluctuations in temperature, capelin biomass and zooplankton, the mean values from the ANOVA model adjusted for effects of area, sex and age was used.

There were a few cases with low number of data points (fish), which make it difficult to obtain precise confidence intervals. For this reason only cases where N>5 data points were included for calculating confidence intervals and graphic presentations of data used in the statistical tests.

3 RESULTS

3.1 Comparing biological characteristics between spring and summer spawning capelin

Size (length and weight)

In male and female capelin total mean length and weight was significantly higher in spring spawners than in summer spawners (ANOVA, P< 0.001) (Figure 7a-b) (Appendix 2 and 3). Length and weight also differed significantly between years in both sexes (ANOVA, P< 0.001).

a.

b.
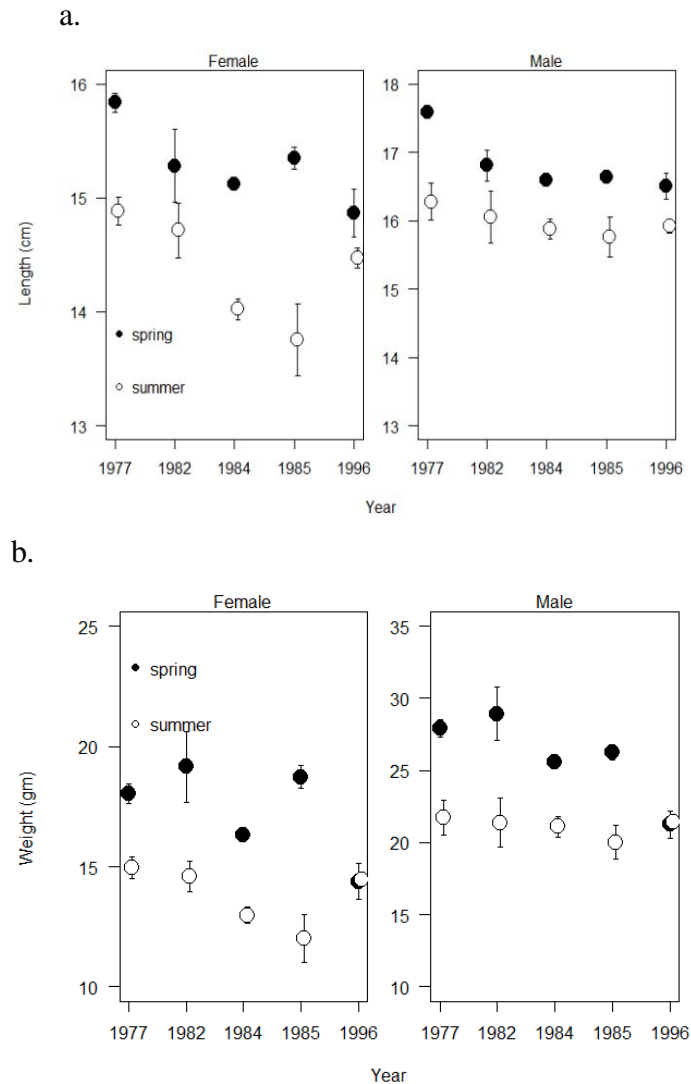
Figure 7a-b: Yearly comparison of length (a) and weight (b) between spring and summer spawning capelin of both sexes. Values given are mean and 95% confidence interval.

Age structure

Age structure was analysed in female and male capelin from the different spawning periods (spring and summer). For all years (1977, 1982, 1984, 1985, and 1996) combined, the distribution of age for both sexes, was significantly different between spring and summer spawners (Kruskal-Wallis, $P<0.001$) (Figure 8a-b) (Appendix 4). There were clear inter-annual differences in age structure, but in general the summer spawners were younger than the spring spawner; summer spawners were predominated by fish at ages 2-3 compared with spring spawners where 4 year olds tended to be most abundant.

a. Female
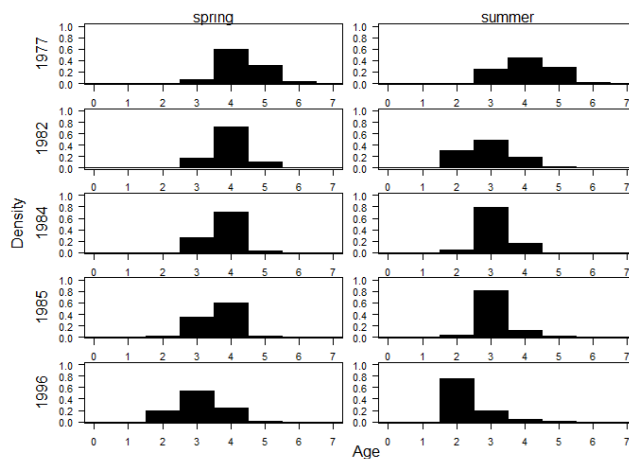
b. Male
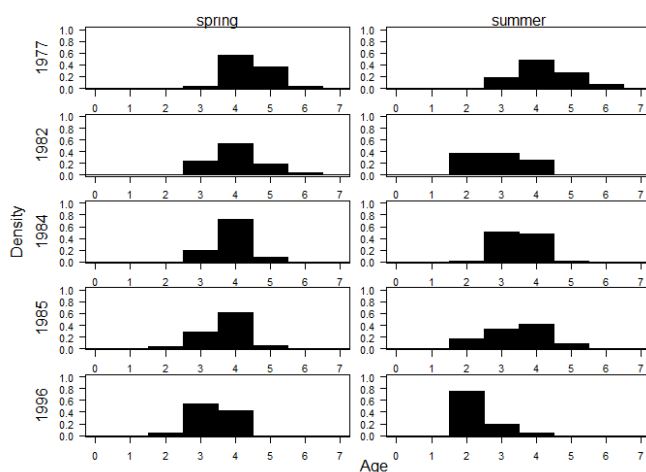
Figure 8 a-b: Age distribution by spawning period (spring and summer) for (a) female and (b) male fish along five different years.

Length at age

Total length at age in spring spawners was significantly higher than in the summer spawners in both sexes (ANOVA, P<0.001) (Figure 9) (Appendix 5). Differences were also found between ages, both in males and females; 4 year old spawners were significantly larger than 3 year old spawners (ANOVA, P<0.001, for female; P<0.01, for male). Also interannual differences in length at age were found in females, highest mean length was observed in 1977 (ANOVA, P<0.001). Length did not differ consistently between spawning periods in different years in both sexes (spawning periods and year interaction, ANOVA, P <0.001). Female capelin of 2-5 years old were typically larger in spring than in summer spawning fish in all sampling years except in 1982 at ages 3 and 4 and in 1996 at ages 2, 3, and 4. A similar trend was found in 2-5 years old male fish except in 1982 at age 4. This result demonstrates that fish which spawned in summer typically had smaller lengths than fish which spawned in spring at the same age in all sampling years except in 1982 and 1996.
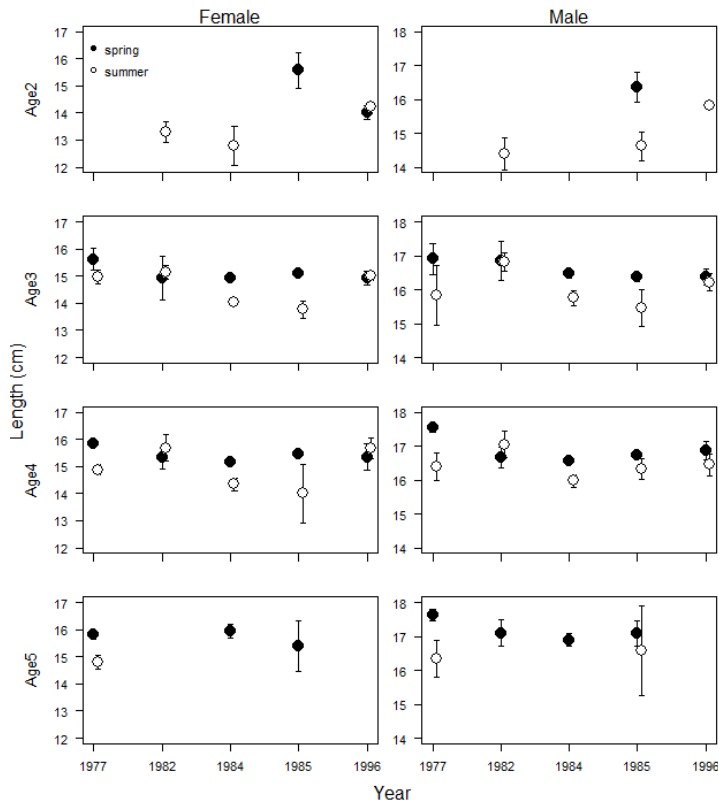
Figure 9: Comparison of length at age between spring and summer spawning capelin of both sexes and different years. Values given are mean and 95% confidence interval.

First year otolith growth

In 2-5 years old male and female, vs1mm was significantly higher in spring than in summer spawners (ANCOVA, P<0.001) (Figure 10) (Appendix 6). Vs1mm also differed significantly with age, with a tendency to decrease from the youngest to oldest spawners in both sexes (ANCOVA, P<0.001). Furthermore, vs1mm differed significantly between years (ANCOVA, P<0.001). Again, in male vs1mm did not differ consistently between spawning periods in different years (spawning periods and year interaction, ANCOVA, P<0.001). Vs1mm was relatively lower in summer than spring spawners in 2-5 years old female in all sampling years except in 1985 at age 3. Similar trend was found in 2-5 years old male in all sampling years except in 1985 at age 2. This result indicates that fish which spawned in spring had relatively higher first year somatic growth than fish which spawned in summer at the same age except in 1985.

In spring, among 3 and 4 years old capelin (all years merged), vs1mm increased with fish size (ANCOVA, P<0.001) (Figure 11) (Appendix 7), whereas such a significant relationship was not found in summer.Vs1mm did not differ consistently between lengths with different spawning periods (length and spawning periods interaction, ANCOVA, P<0.001 for age 3; P<0.05 for age 4) (Figure 11). This result suggests that first year otolith growth (vs1mm) generally increases with fish size in spring spawners, but not in summer spawners.

Vs1mm measured at the same year, sex, age and length was significantly higher in spring spawners than in summer spawners using the 1984 as a test year (GLM, P< 0.001) (Figure 12 a-b) (Appendix 8). Same model also showed that vs1mm significantly differed with length in 1984 (GLM, P<0.001). Looking more closely at 3 and 4 years old fish in 1984, vs1mm increased with increasing length in both sexes of the spring spawners. A similar trend was observed for spring spawners in 1985, whereas for summer spawners (1984 only) vs1mm decreased with increasing length at age 4.
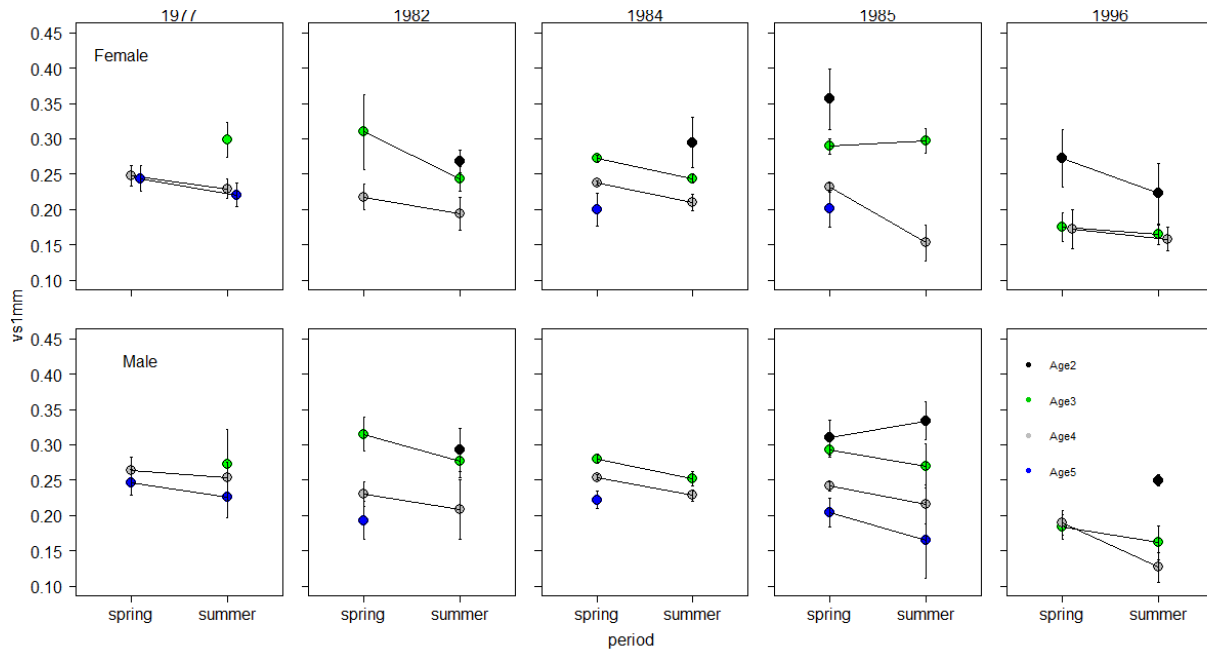
Figure10: Comparison of first year otolith increment (vs1mm) between spring and summer spawning capelin of both sexes and different years and ages. Values given are mean and 95% confidence interval.

Figure 11: Relationship between fish length and first year otolith increment (vs1mm) at ages 2-5 between spring and summer spawning capelin of both sexes. Values given are mean and 95% confidence interval.

a. Age 3

b. Age 4
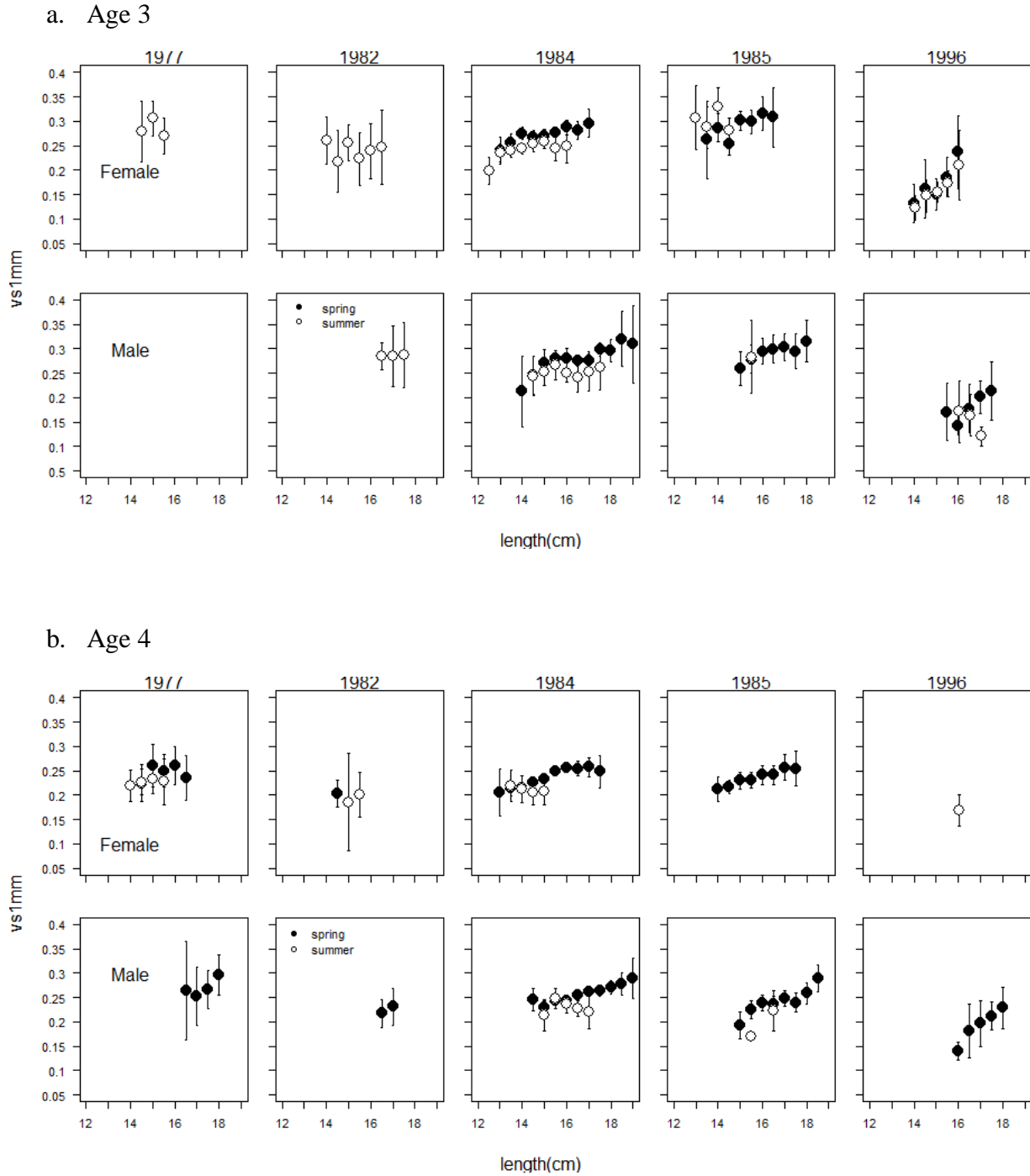
Figure 12a-b: Comparison of first year otolith increment (vs1mm) by body length between spring and summer spawning capelin of both sexes and ages 3 (a) and 4 (b) years. Values given are mean and 95% confidence interval.

Ratio between first and second year otolith growth

In 2-5 years old female and male, vs1mm/vs2mm was significantly higher in spring than summer spawners, (ANCOVA, P< 0.001) (Figure 13) (Appendix 9). Vs1mm/vs2mm was significantly different with age and year (ANCOVA, P<0.001). Vs1mm/vs2mm did not differ consistently between spawning periods in different years in both sexes (spawning periods and year interaction, P<0.01 for female; P<0.001 for male). Female spring spawning capelin of 2-5 years old had larger vs1mm/vs2mm than the summer spawning capelin in all sampling years except in 1985 at age 3 and in 1996 at ages 3 and 4. Similar trend was found in 2-5 years old male in all sampling years except in 1977 at age 4 and in 1996 at ages 3 and 4.

In 3 and 4 years old capelin (all years merged) vs1mm/vs2mm did not significantly increase with length (Figure 14) (Appendix10). Also within spring spawning capelin no significant trend existed between vs1mm/vs2mm and length. Similarly, no significant trend was found between length and vs1mm/vs2mm in summer spawning fish, with exception at age 4. This result demonstrates that ratio between first and second years otolith growth (vs1mm/vs2mm) does not generally increase with fish size in spring and summer spawning fish.

Vs1mm/vs2mm measured at the same year, sex, age and length was significantly higher in spring spawners than summer spawners, and vs1mm/vs2mm was significantly higher at age 4 than age 3 in the test year 1984 (GLM, P<0.001) (Figure 15 a-b) (Appendix 11). Vs1mm/vs2mm did not significantly differ with length in 1984. In 3 year old male and female, no specific trend was found in vs1mm/vs2mm with increasing length in both spawning periods in 1984. At age4, vs1mm/vs2mm increased with increasing length in summer spawning female and vs1mm/vs2mm decreased with increasing length in male in the same year.
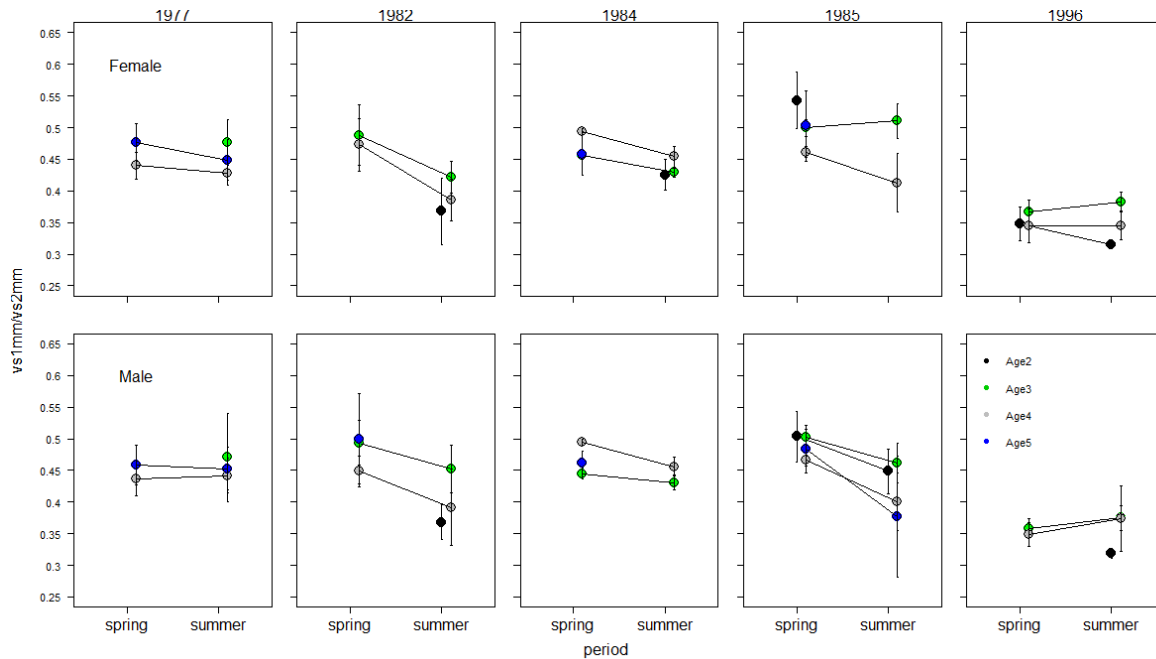
Figure 13: Comparison of ratio between first and second year otolith growth (vs1mm/vs2mm) among spring and summer spawning capelin of both sexes and different years and ages. Values given are mean and 95% confidence interval.
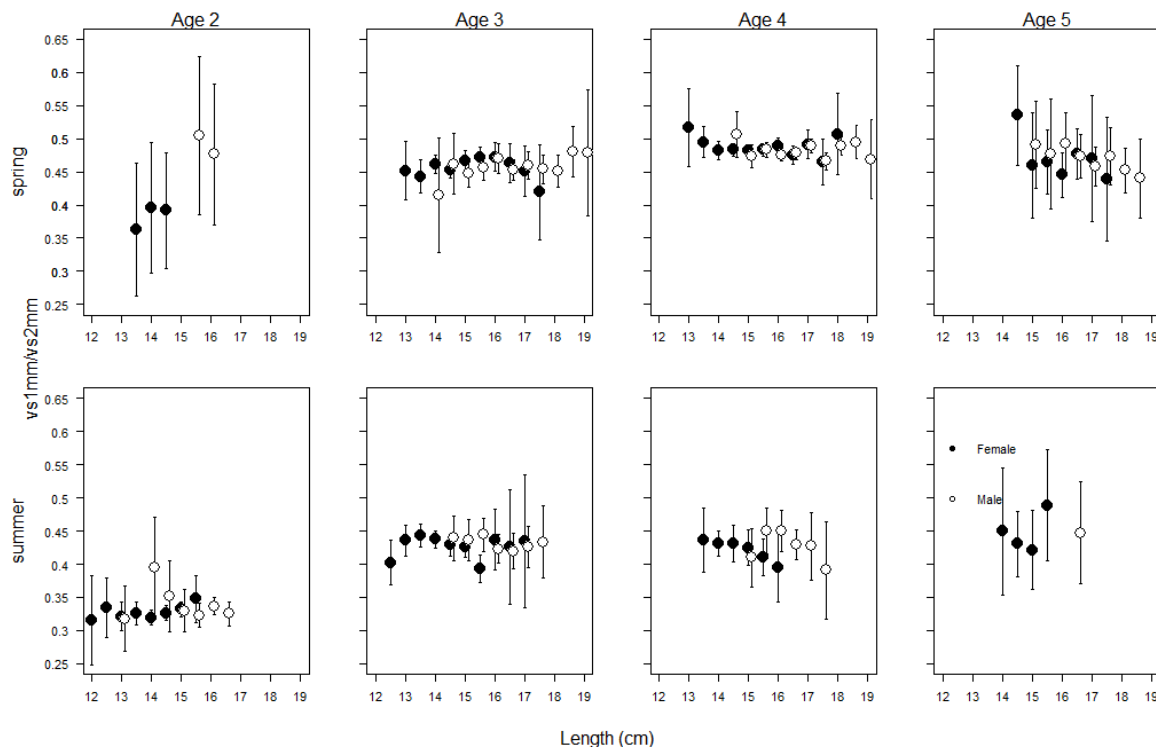
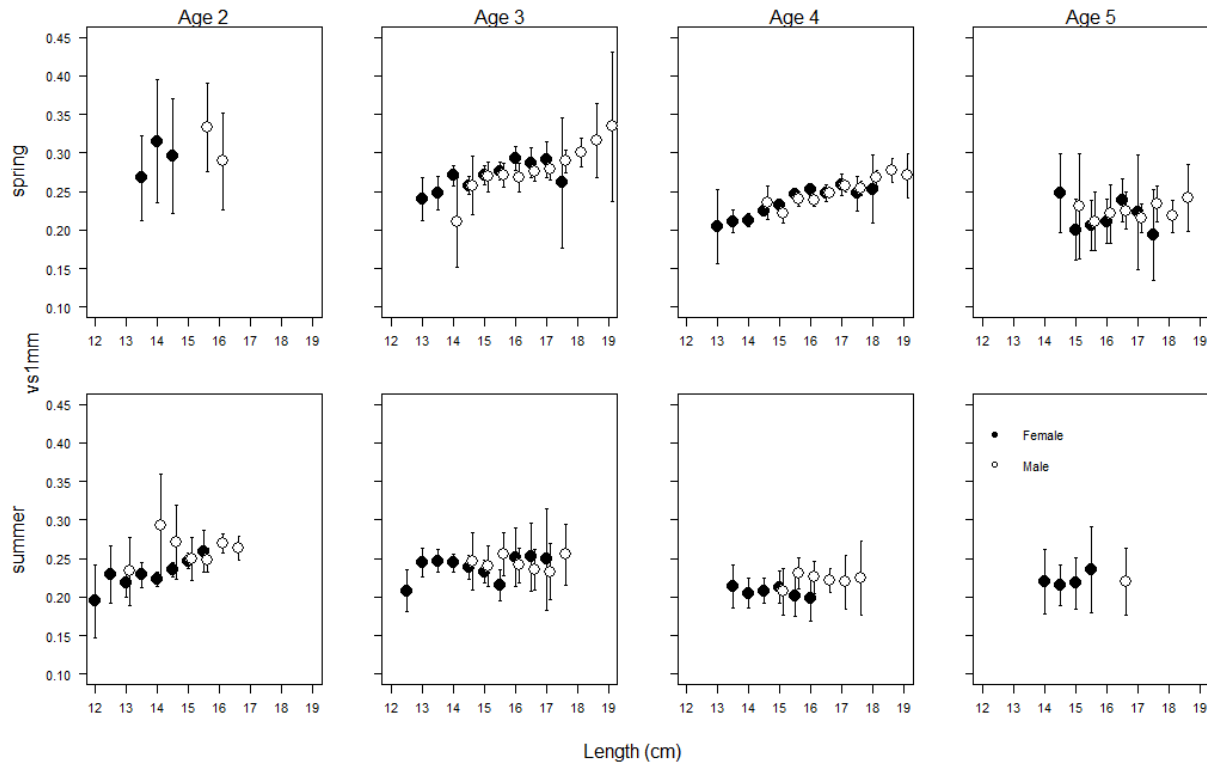**Figure 14:** Relationship between fish length and ratio between first and second year otolith increment (vs1mm/vs2mm) at ages 2-5, spring and summer spawning capelin and both sexes. Values given are mean and 95% confidence interval.

a. Age 3
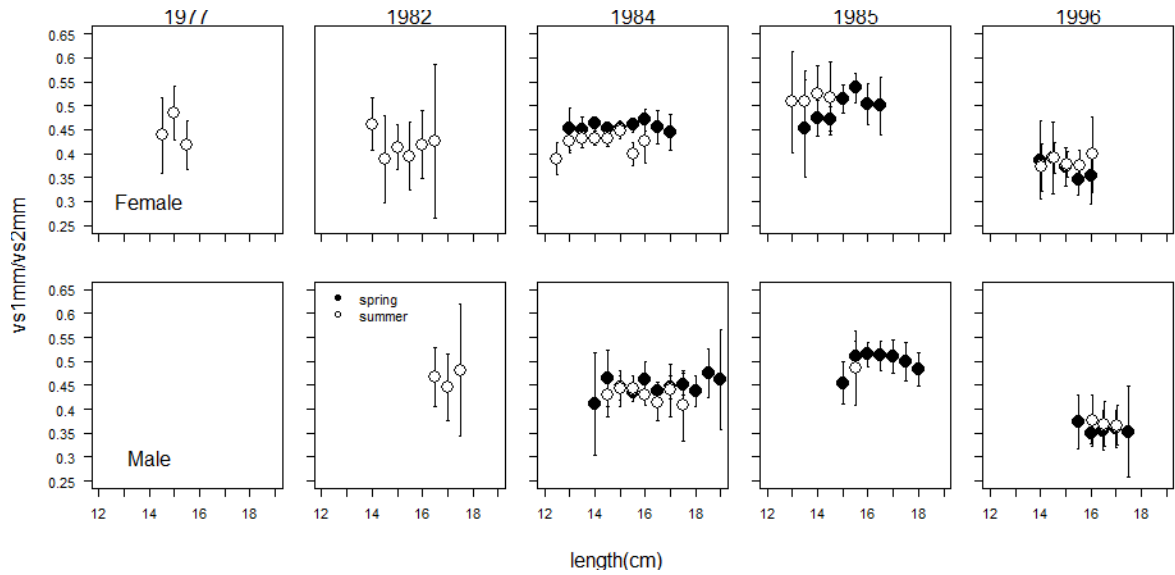
b. Age 4
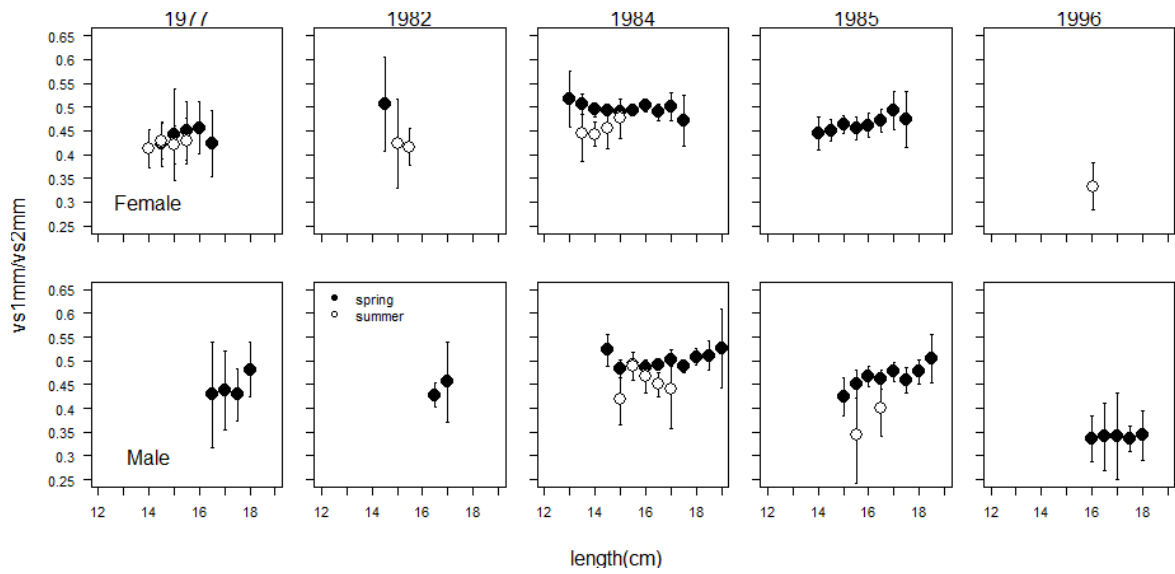
Figure 15a-b: Comparison of ratio between first and second year otolith growth (vs1mm/vs2mm) by body length between spring and summer spawning capelin of both sexes and ages 3 (a) and 4 (b) years. Values given are mean and 95% confidence interval.

Condition (weight-at-length)

Condition in terms of weight-at-length was significantly higher in spring than summer spawning capelin (GLM, P<0.001) (Figure 16) (Appendix 12). Weight-at-length was also significantly higher in male than female capelin (GLM, P<0.001). Moreover, weight-at-length was also significantly different by year (GLM, P<0.001).
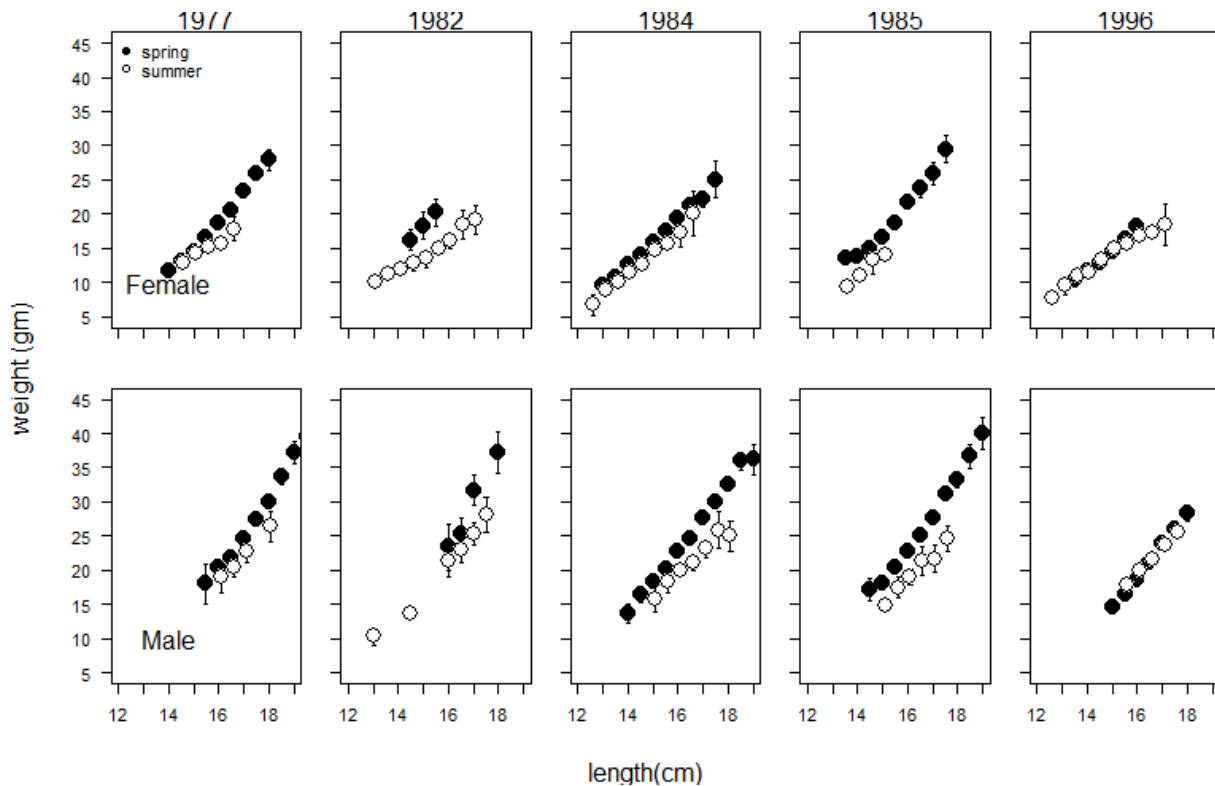
Figure 16: Yearly comparison of condition (weight-at-length) between spring and summer spawning capelin of both sexes. Values given are mean and 95% confidence interval.

3.2 Geographical distribution of capelin in the Barents Sea related to otolith growth

First year otolith growth (vs1mm) averaged overall years in bins of 1 degree on the latitudinal range and 2 degrees on the longitudinal range and GIS mapping demonstrated clear geographical differences changing with age (Figure 17). It was a clear tendency that vs1mm decreased towards the south east for the 1-2 years old. However, at ages 3-5 this geographical trend faded out at the same time as vs1mm decreased all over the area, indicating that individuals with high

vs1mm spawned at ages 3-4 and was not part of the remaining population feeding in the autumn at ages 4-5.

The trends in vs1mm observed with GIS mapping were further explored with statistical analyses on data split into a northern (latitude>75°N) and southern (latitude$\leq$ 75°N) areas. Here, vs1mm significantly differed with longitude but covariates age and area was also significant (ANCOVA, P<0.001) (Figure 18) (Appendix 13). Accordingly, vs1mm was significantly lower in the southern area than northern area for ages 1-2 (t-test, p<0.001), but not for ages 3-5 (Appendix 14). At age 1 and 2, in the northern and the southern areas vs1mm significantly decreased with longitude (linear regression, P<0.001). But at age 3 and 4 (age 5 did not include due to few data points), in the northern and the southern areas, vs1mm was not significantly different with longitude (Appendix 15). These results support the results from GIS mapping, and indicates that in general capelin with the smallest first year otolith increment (vs1mm) is distributed to the south east as 1-2 year olds, but this trends fades out as individuals with the highest vs1mm leaves the rest of the populations to spawn and die.
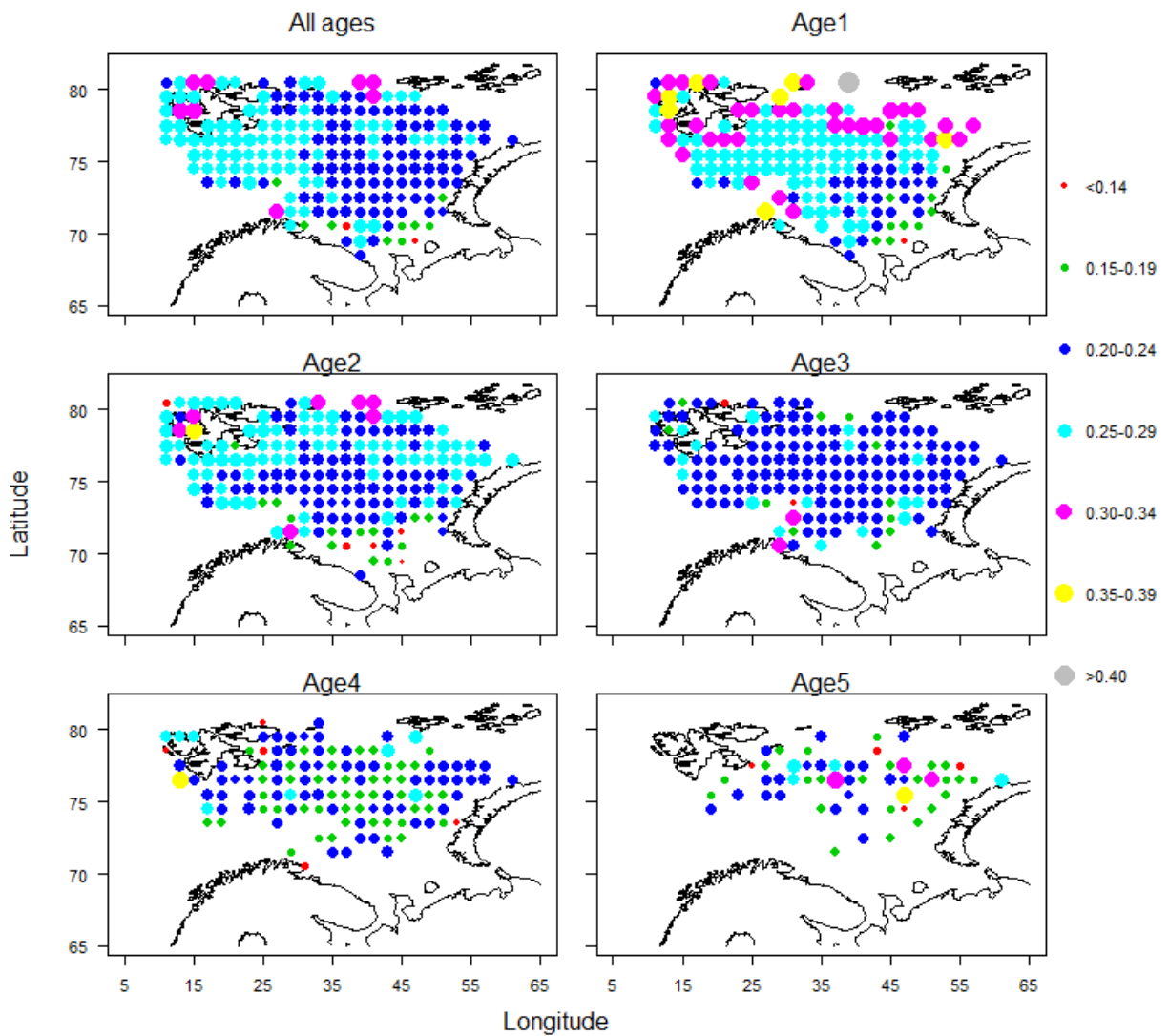
Figure 17: Geographical mapping of mean first year increment growth (vs1mm) of capelin in the Barents Sea over the study period 1976-2012 (August-October)
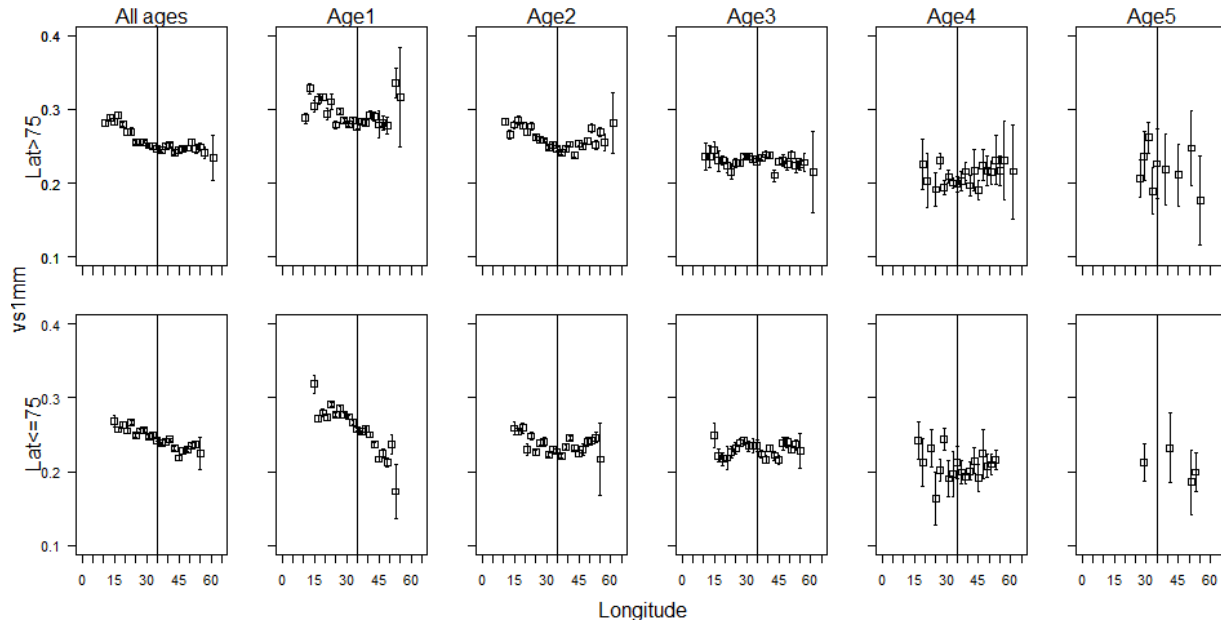
Figure 18: Relation between first year increment size (vs1mm) and longitude for 1-5 years old capelin in southern and northern Barents Sea. Data are pooled for the study period1976-2012 (August-October). Values are given mean and 95% confidence interval.

Ratio between first and second year otolith growth (vs1mm/vs2mm) averaged overall years in bins of 1 degree on the latitudinal range and 2 degrees longitudinal range and GIS mapping demonstrated clear geographical differences changing with age (Figure 19). It was a clear tendency that vs1mm/vs2mm was decreasing southwards for the 2 year old capelin. However at ages 3-5 this geographical trend faded out the same time as vs1mm/vs2mm decreased all over the areas indicating that individuals with high vs1mm/vs2mm spawned at ages 3-4 was not part of the remaining population feeding in the autumn at ages 4-5.

The trends in vs1mm/vs2mm observed with GIS mapping were further explored with statistical analysis on data split into a northern (latitude>75°N) and southern (latitude≤75°N) areas. Vs1mm/vs2mm did not differ significantly with longitude (Figure 20). However, vs1mm/vs2mm differed significantly with age and area (ANCOVA, P<0.001) (Appendix 16). Vs1mm/vs2mm was significantly lower in the southern areas for age 2 (t-test, P<0.001) but not for ages 3 and 4 (age 5 did not include due to few data points) (Appendix 17). This result indicates that capelin with smallest ratio between first and second years otolith increment (vs1mm/vs2mm) has a tendency to be distributed in the southern part of the Barents Sea at age 2.

34
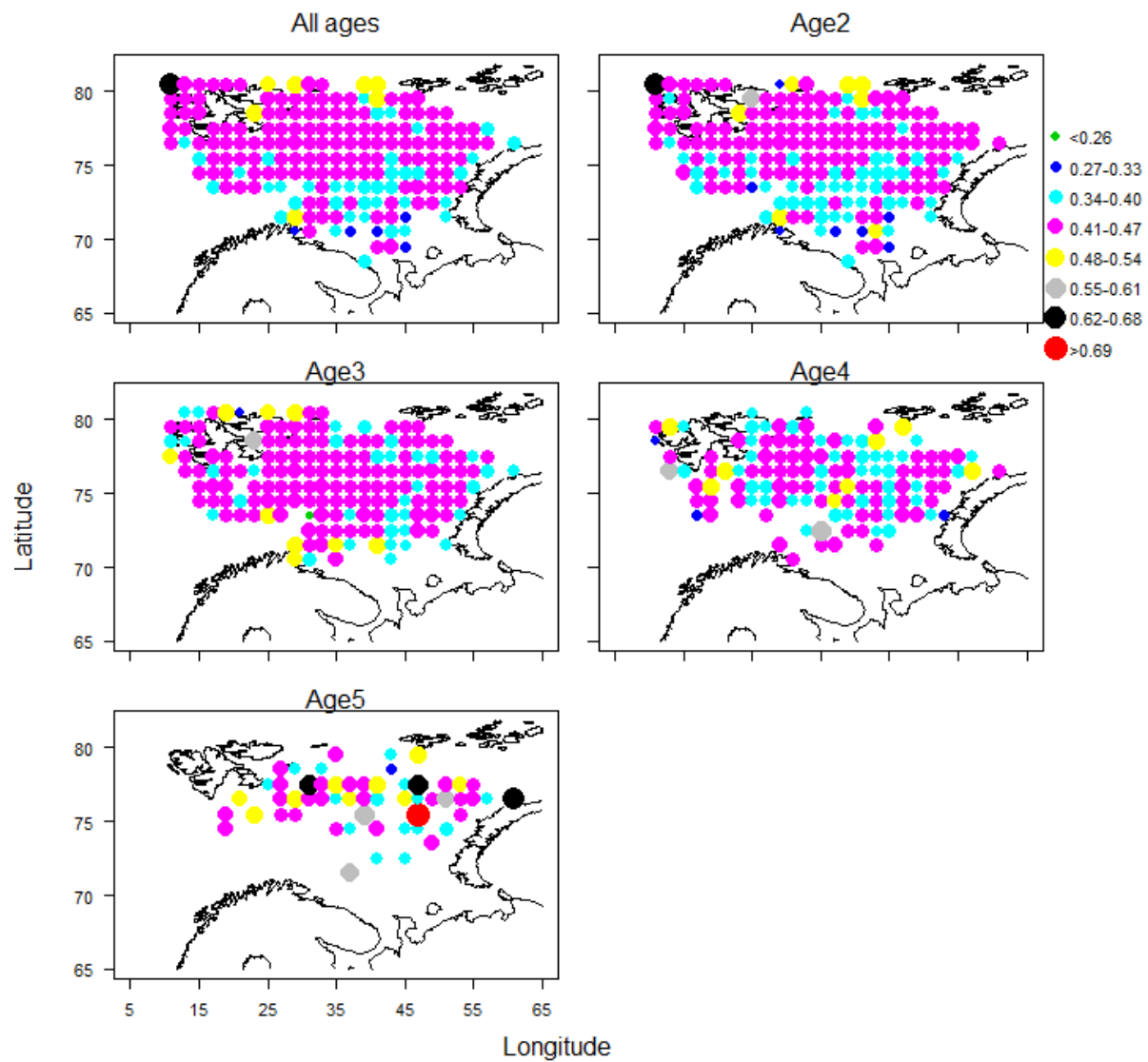
Figure 19: Geographical mapping of mean ratio between first and second year increment growth (vs1mm/vs2mm) of capelin in the Barents Sea over the study period 1976-2012 (August-October).
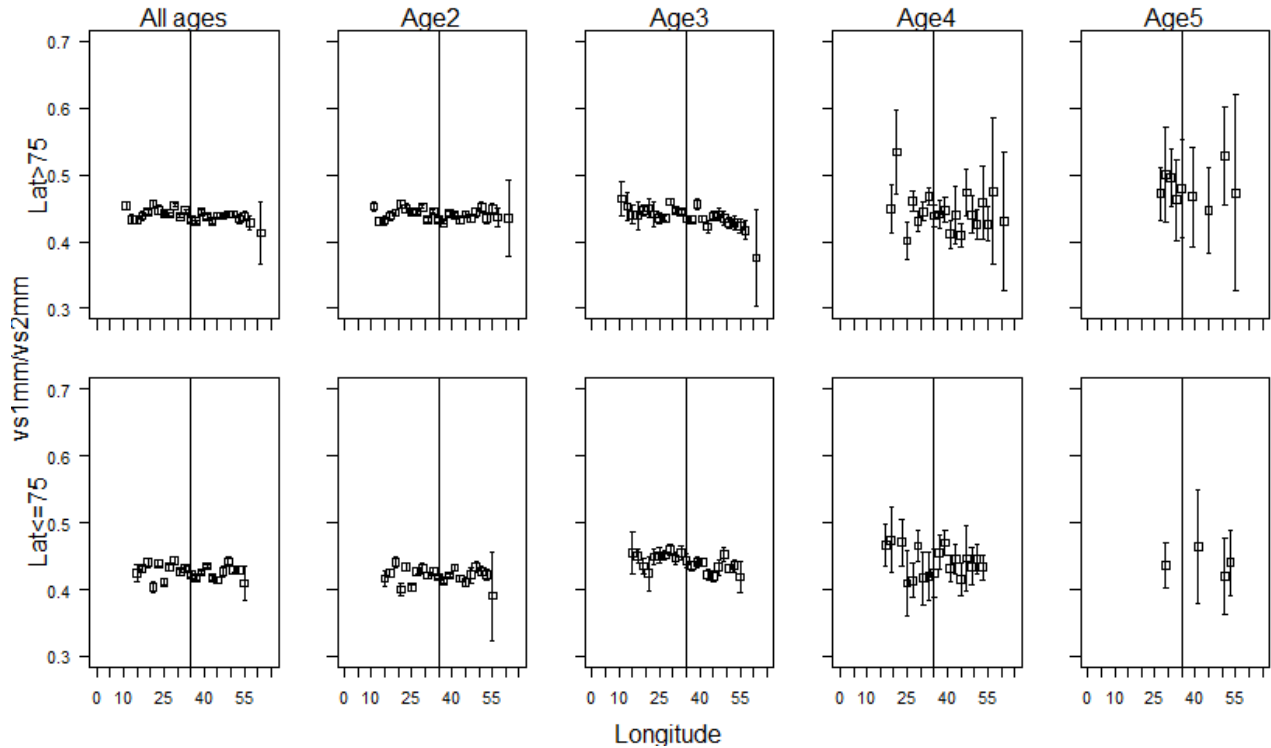
Figure 20: Relationship between ratio of first and second years otolith growth (vs1mm/vs2mm) and longitude for 2-5 years old capelin in the southern and northern Barents Sea. Data are pooled for the study period 1976-2012 (August-October). Values are given mean and 95% confidence interval.

3.3. Interannual variations in otolith growth of capelin in different areas related to temperature, zooplankton and capelin stock size

Interannual variations of vs1mm of 1-3 years old capelin was analysed in four different areas (NW, NE, SW, SE), and vs1mm was significantly different with year, area, age and sex (ANOVA, $P<0.001$) (Figure 21) (Appendix 18). In the northern and the southern areas the largest size vs1mm was observed at age 1. In the northern area (NE, NW), vs1mm peaked during 1984, 1989, and 2006 whereas in the southern area (SE, SW), vs1mm peaked in 1985, 1990 and 2006.

a. Female
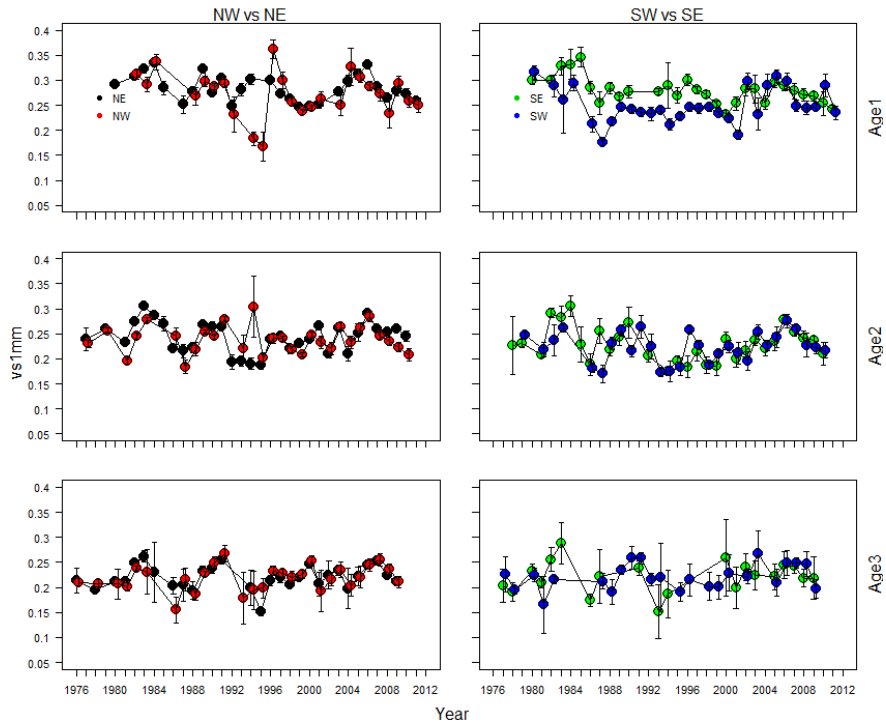
b. Male
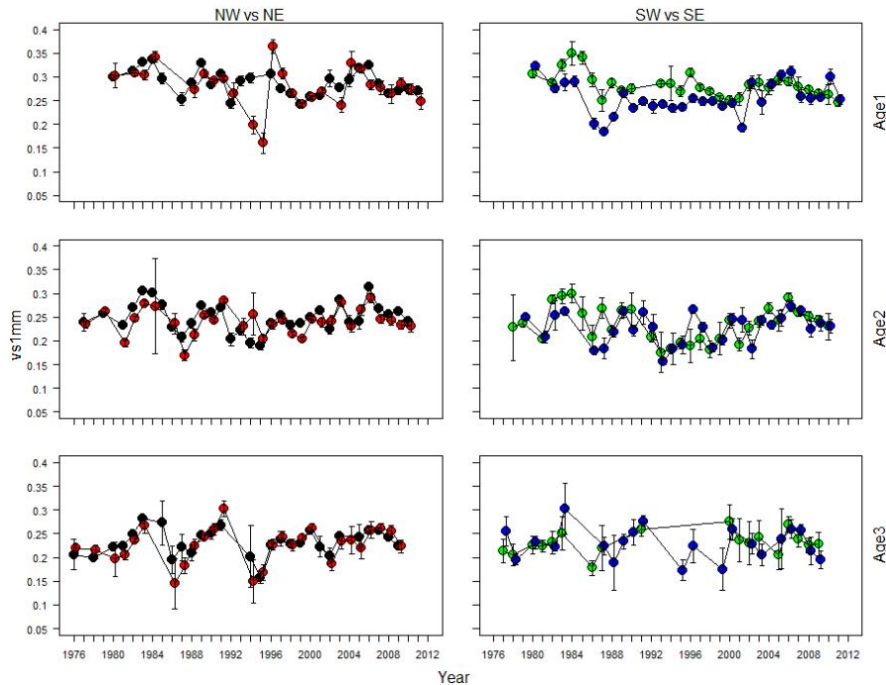
Figure 21: Interannual variations in first year increment (vs1mm) of 1-3 years old capelin (a) female and (b) male in different areas of the Barents Sea. Data are pooled for the first year increment formation period 1976-2012 (August, September, and October). Values given are mean and 95% confidence interval.

Interannual variations of vs1mm/vs2mm of 2-3 years old capelin was analysed in four different areas (NW, NE, SW, SE) and vs1mm/vs2mm was significantly different with year, area, and sex (ANOVA, $P<0.001$ for area; $P<0.01$ for year, $P<0.05$ for sex) (Figure, 22a-b) (Appendix 19). In female and male, in the northern area (NE, NW), vs1mm/vs2mm peaked during, 1983, 1991, and 2007. In the southern area (SE, SW), vs1mm/vs2mm peaked in 1976, 1983, and 1990 in female whereas in male it peaked during 1976, 1983 and 2000.

a. Female
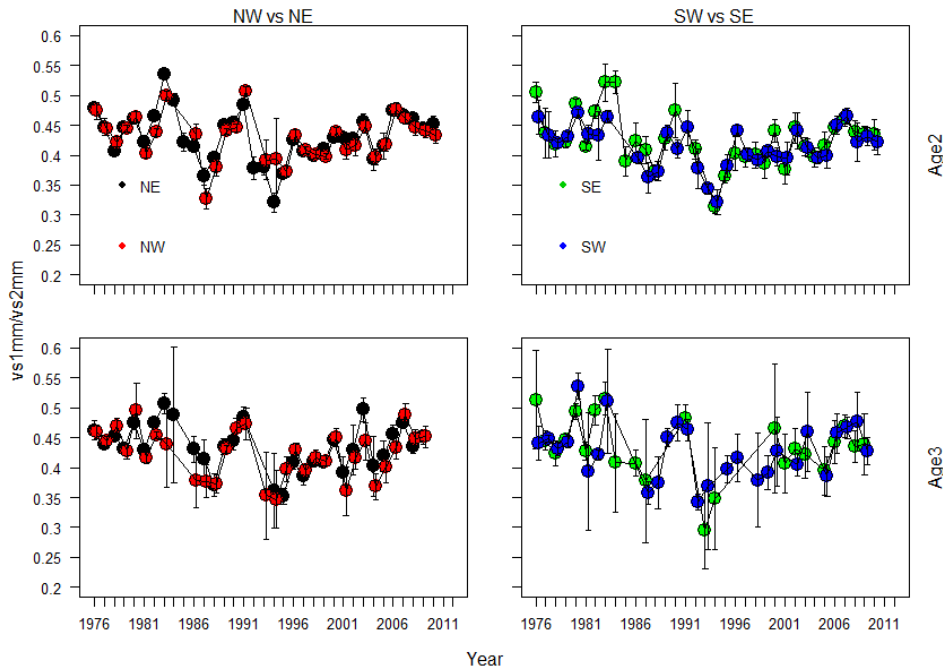
b. Male
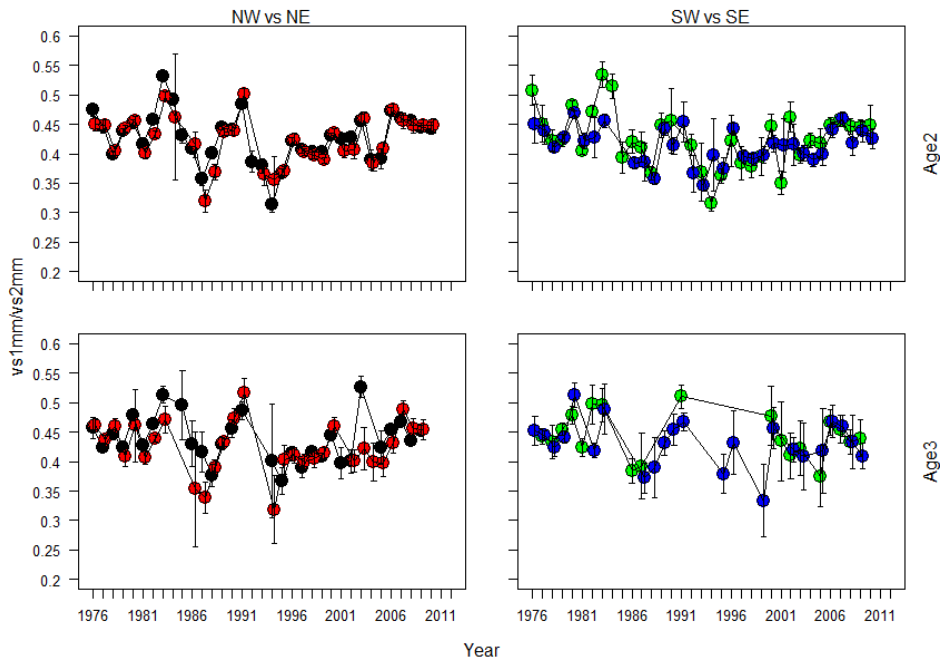
Figure 22 a-b: Interannual variation in ratio between first and second year increment size (vs1mm/vs2mm) of 2-3 years old capelin (a) female and (b) male in the different areas of the Barents Sea. Data are pooled for the ratio between first and second year otolith formation period 1976-2012 (August, September, and October). Values given are mean and 95% confidence interval.

Vs1mm was significantly different with temperature, capelin biomass, zooplankton, areas, ages and sex (ANOVA, P<0.001) (Figure 23) (Appendix 20). Vs1mm/vs2mm was significantly different with temperature, capelin biomass, zooplankton, areas and sex (ANOVA, P<0.001) (Appendix 20). A closer look of the intaerannual variation in temperature showed periodic changes similar to growth of vs1mm.
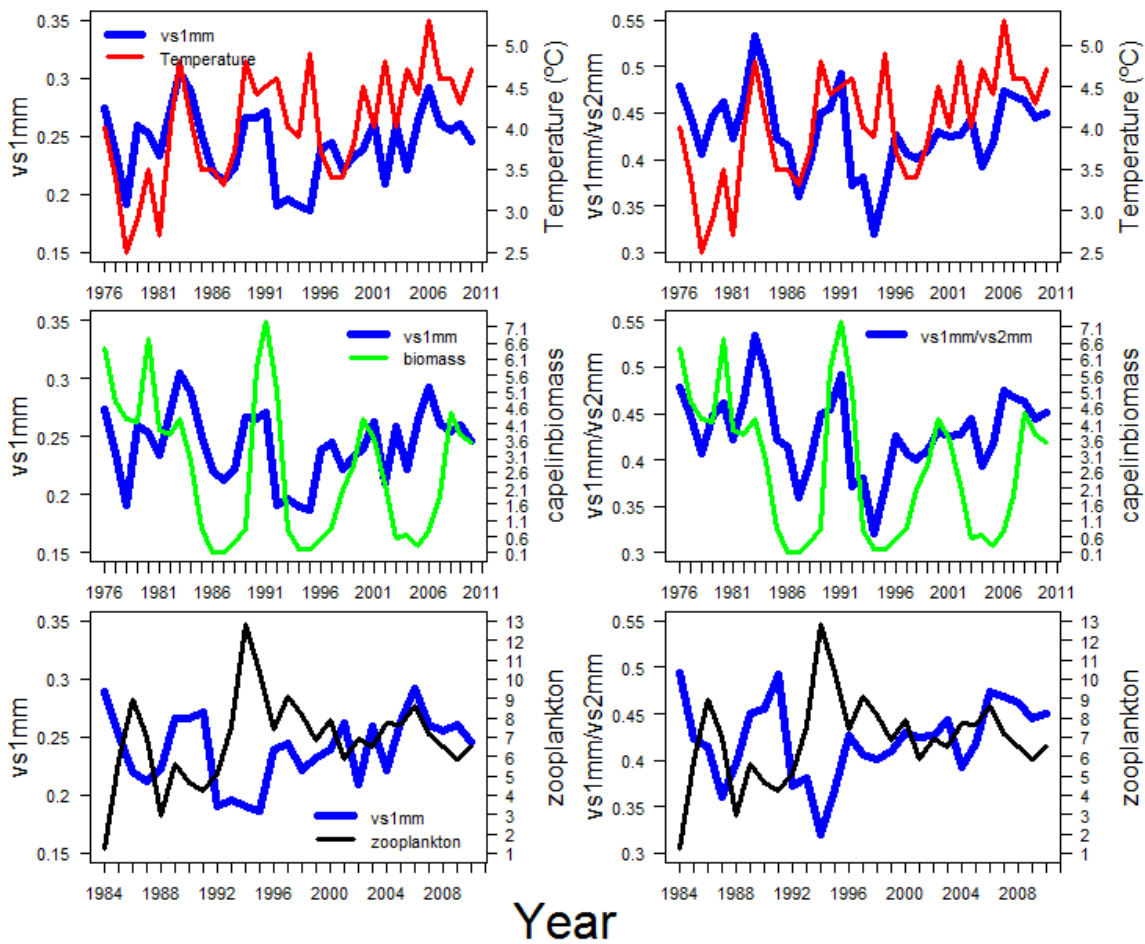
Figure 23: Comparison of adjusted (for effects of area, age and sex) mean first year increment size (vs1mm) and ratio between first and second year increment size (vs1mm/vs2mm) with yearly temperature (Kola section), capelin biomass and zooplankton corresponding to vs1mm and vs1mm/vs2mm formation in the Barents Sea.

4 DISCUSSION

The analyses of the present thesis have addressed the potential factors leading to variation of spawning time of the Barents Sea capelin, with special emphasis on the question whether seasonal timing of spawning to spring or summer is due to an established strategy or simply a result of environmental conditions. The analyses were carried out in three steps: Firstly, biological characteristics were compared between spring and summer spawners. Secondly, the distribution of capelin related to these characteristics during the autumn feeding period in the Barents Sea in the years prior to spawning were analysed. Thirdly, interannual variations in these characteristics were analysed in relation to stock density and environmental factors. In the following I will discuss the results from these three main analyses. Based on this discussion I will also answer the question; why does capelin spawn both in spring and summer? Finally I will discuss future potential research that may further improve the understanding of timing of spawning in capelin

4.1 Biological differences between spring and summer spawning capelin

The present thesis demonstrated that in capelin the summer spawners are significantly younger and smaller (lower length and weight) then spring spawners. Previous research also shows that timing of spawning may depend on the size or age of spawners (Marteinsdottir and Björnsson, 1999). It is evident that large size fish reaches to the coast earlier for spawning than the small and young fish and size-dependent maturation may be associated with this (Slotte *et al.*, 2000). This hypothesis is also common in Pacific herring (Ware and Tanasichuk, 1989), and capelin (Templeman, 1948; Vandeperre and Methven, 2007). Accordingly, Flynn and Burton (2003) found that more advanced stage gametogenesis was observed in large size male and female than relatively small size capelin and as a result, large size fish are able to spawn earlier than smaller one. Also, in cod timing of spawning is associated with age (Hutchings and Myers, 1993). It is also evident in the Barents Sea cod stock, early spawning was observed in larger and older cod than first time spawners (Hutchings and Myers, 1993).

The summer spawners analysed in the present study were also characterised by a slower somatic growth as well as a smaller first year otolith growth and ratio between first and second year otolith growth than in spring spawning capelin. Hypothetically capelin hatched in summer would on average have both a lower first year otolith growth and a lower ratio between first and second year otolith growth than capelin hatching in spring due to a much shorter feeding season in their first year of life. Hence, the observed differences in biological characteristics could be interpreted as capelin returning to spawn in the same season they hatched themselves as genetically (parentally) determined effect, i.e. that summer spawning is an established strategy as suggested in spring and summer spawning herrin (Husebø *et al.*, 2005). Environmental factors are responsible for the first year otolith growth. Like fish larvae, otolith microstructure formation also depends on many factors such as food availability, photoperiod, temperature and salinity (Ivajord *et al.*, 2008). Among these factors, temperature and food availability play a pivotal role for the formation of increment (Folkvord *et al.*, 2004). Hence, for capelin it may not only be a short feeding period when hatching in summer, but the availability of suitable food for larvae may not be as good as for larvae hatching in spring. This is supported by other studies suggesting that late spawning in fish may have negative impact on early life stages. For example, larvae of the Baltic cod usually eat nauplii during spring, and this food habitat changes to copepodites and adult copepods in summer (Zuzarte *et al.*, 1996), suggesting that this prey of right size is not available for late hatching offspring. In addition, larvae which are hatched early may be benefited in terms of reduced predation compared with late hatched larvae as suggested in herring (Husebø *et al.*, 2009). The importance of first year growth for age of spawning as been demonstrated in another study, where it was suggested that fish with better first year growth could be able to exploit energy for the development of gonads and as a result they will be recruited as early spawners (Eklund *et al.*, 2001).

According to this study, the condition (weight at length) in summer spawning capelin was worse than spring spawning capelin. There could be two potential explanations to this result. First, this could be a result of a longer time gap between feeding period (year prior to spawning) and until spawning, which may cause a higher reduction in weight from last feeding to until spawning. This is likely as the main feeding season is from July-October, and summer spawners may have very little to eat during April due to the fact of ice-cover period which cause less availability of food in the Barents Sea. Another explanation may be that the summer spawners have lived under

worse feeding conditions in the year prior to spawning, as indicated by the observations of differences in somatic and otlith growth. This is important as the body condition and maturation may be strongly related. Condition has been suggested to be an important factor for timing of spawning in capelin (Davoren *et al.*, 2012). Also in herring bad condition of Norwegian spring spawning herring during pre-spawning stage was responsible for late maturation (Slotte *et al.*, 2000). Moreover in cod, rate of maturation is increased due to better condition (Kjesbu, 1994). Rajasilta argued (1992) that among the early and late spawners of Baltic herring there was a large variation of fat content, where herring which store high fat during December will spawn early whereas herring with low fat would spawn late. In order to explore whether it is likely that capelin summer spawners have lived under worse growth conditions then the summer spawners, there is need for more knowledge of their feeding distribution, food availability and the related temperature conditions, which will be discussed next.

4.2 Distribution variation among spring and summer spawning capelin during feeding period

This study has found that 1-2 years old capelin with small first year otolith growth and lower ratio between first and second year otolith growth were distributed in more to the southern and eastern parts of the Barents Sea during autumn, which could be interpreted as summer spawners having a more south eastern distribution than spring spawners. Also the data collected from selected years with summer spawners for biological comparisons with spring spawners indicate a more eastern spawning distribution of summer than spring spawners, supporting that summer spawners may arrive from more eastern feeding grounds. This south eastern distribution of capelin during feeding season may clearly have impact on both the somatic growth, condition and consequently spawning time of capelin. The fish which had resided in these areas usually had a poor growth (Skjoldal, 1992). Skjoldal (1992) has argued that small somatic growth was observed in the south east part of the Barents Sea due to availability of low amount of zooplankton. For example, during 1987 biomass of zooplankton was low and as a result, poor growth was observed in capelin. Moreover, Gjøsæter (1986) found a strong positive relation between growth and feeding area in the Barents Sea capelin. Another study found that during 1994 and 1996, growth in capelin was lower in the south eastern parts of the Barents Sea

(Gjøsæter, 1999). Similarly, in 1990, during autumn, the distribution of capelin moved to south and east due to cooler water temperature which caused late spawning in Newfoundland capelin in 1991 (Lilly, 1994). Similarly, late spawning of the Barents Sea capelin was linked to a change in autumn distribution (Bakanev and Sergeeva, 1994; Miller, 1994). Again, larvae of summer spawners may have a tendency to be distributed south east due to change of winds and currents. One study demonstrated that if hatching occurs early in a season (spring), larvae move more to northwards. On the other hand, if hatching occurs late in the same season larval move towards the same area become weaker due to weak and less unidirectional wind (Vikebo *et al*., 2010) while, in summer, when wind is even weaker than spring, capelin larvae disperse towards south east. This gives further support to the conclusion that the occurrence of spawning in both spring and summer is due to established strategies, different larval drift, different nursery areas and growth conditions.

According to this study, 1 and 2 years old small capelin were distributed in the south east parts of the Barents Sea whereas, large capelin distributed in the northern part of the Barents Sea. But, when capelin reached 3-5 years old, small size capelin were distributed throughout out the Barents Sea which indicates that large size capelin spawned early at ages 3 and 4. As a result, they are not observed with the remaining population in the autumn at ages 4-5. Usually, capelin starts to mature during late summer. Thus, during feeding season it is possible to identify mature capelin which will spawn in next year. During feeding time, capelin which is mature generally moves more to the northern part of the Barents Sea than immature capelin (Gjøsæter, 1999).

4.3 Interannual variation in growth, climatic conditions and spawning timing of capelin

The result of the present study indicates that capelin growth varies interannually and that this may be linked with temperature, stock abundance and zooplankton. This is a similar result as in Gjøsæter (1998), concluding that growth variation is the result of temperature change, abundance of zooplankton or both at the same time (Gjøsæter, 1998). As a result different types of physiological process like growth could be affected by temperature (Brett, 1979; Jobling, 1994). Previous study has also found a large variation in capelin growth during late 1970s and the 1980s (Skjoldal *et al*., 1992). During this period lowest growth was observed in 1977 and negative

anomalies were responsible for this poor growth. Gjøsæter and Loeng, (1984) also found a positive relationship between temperature and capelin size, capelin size increases with increasing temperature. In the Norwegian coast, temperature plays a significant role in the growth of juvenile Norwegian spring spawning herring (Husebø, *et al.*, 2007). Similar relationship is found in other species like sprat (Mölmann *et al.*, 2005), Japanese mackerel (Watanabe and Yatsu, 2000) and Arctic cod (Ottersen and Loeng, 2000).

According to this study, close to the end of the study period (i.e. in 2005) capelin biomass was low and growth of capelin was high. Another study has also found a similar correlation between biomass and growth. For example, Gjøsæter (1999) found that there was a highly significant negative correlation between growth rate and stock size of capelin in the Barents Sea. Small stock size is responsible for high growth rate. When the stock size is large, it is necessary to extend the feeding area to fulfill the demand of food (Gjøsæter, 1999) whereas, no food limitation is observed when stock density is small.

According to this study, growth peaked when temperature was high since food availability depends on temperature which can lead indirect effects on growth (Gjøsæter and Loeng, 1987). One study revealed that low amounts of food are available due to low temperature. Therefore, slow growth is observed which lead late maturation of capelin (Nakashima, 1996). Hay (1985) revealed that a positive relationship exists between maturation of fish and temperature. Hydrographic condition and availability of nutritious organism could be changed with the change in climate which can make adverse impact on the growth of different organisms in food cycle (Gjøsæter and Loeng, 1987). For example, in the Atlantic and Arctic water, abundance of zooplankton and relatively high growth of capelin is linked to temperature (Orlova *et al.*, 2005, 2010; Gjøsæter and Loeng, 1987; Gjøsæter *et al.*, 2002). Lipid-rich euphausiid's stock increased in the Barents Sea due to the increase of temperature (Dalpadado *et al.*, 2012). Norwegian spring spawning herring grow fast due to the favorable condition of nursery grounds and this type of herring are recruited very early for spawning than the population which have slow growth (Holst and Slotte, 1998). Growth variation was also observed in herring's larvae in different nursery areas in the Celtic Sea, West Irish Sea and East Irish Sea. Among these three seas the largest larvae were found in the Celtic Sea, the medium and small size larvae from East Irish Sea and

the West Irish Sea. Generally, abiotic and biotic factors are responsible for different growth rate among the three nursery grounds. Here, large size herring of the Celtic sea spawned early at age 1 whereas slow growing herring in the West Irish Sea delayed spawning until at age 2 (Brophy, 2003). In the Pacific herring maturity depends on temperature and feeding also has influence on maturation (Hay and Brett, 1988). Aneer (1985) revealed that nutritional condition determines the time of spawning in Baltic herring. Laine and Rajasilta (1998) showed that spawning time variation is the result of the variation of environmental conditions and zooplankton abundance during spawning period. However, spawning time may changes within a season due to fluctuation of environmental condition though it could not vary from spring spawning period to summer spawning period. For example, during 1991-1994, spawning period was changed in Newfoundland capelin due to low water temperature and small mean size of capelin. As a result, spawning occurred one month later than previous year (Carscadden *et al.*, 1997).

4.4 Why does capelin spawn both in spring and summer?

Given the described links found between temperature, zooplankton and growth of fish in general, and the observations of slow growth of capelin in the south eastern Barents Sea linked to lower zooplankton availability, it seems likely that the observed fluctuations in growth of the present study linked to external factors may have resulted in interannual variations in age at spawning as well as timing of spawning within a spring spawning or summer spawning season. However, it is not likely that such climatic variations may explain why we have spring and summer spawners. It is a main conclusion of the present thesis that the occurrence of spawning in both spring and summer is due to established strategies, ending in different larval drift, different nursery areas and growth conditions, which consequently leads to spawning at smaller sizes, younger ages and in lower condition. The fact that spawning season is something that is a genetically (parentally) determined is supported in other studies. One study found that the timing of spawning in herring appears to be genetically determined (Haegele and Schweigert, 1985). Another study, through analysing the first year growth of the Archipelago's herring, concludes that offspring of the early spawning fish also spawn early (Eklund *et al.*, 2001). Also in Celtic herring, it was evident that the season of hatching determines spawning time (Brophy 2006). Brophy (2006) further concluded that in herring shifting of spawning time was very low, and Husebø *et al.* (2005) also

reached the same conclusion on spring and summer spawning herring in Norwegian waters. It is likely that the explanations to different spawning seasons in herring also is attributable to the Barents Sea capelin, suggesting that it is not likely that a capelin hatched in spring will spawn in summer regardless of climatic fluctuations. However, one cannot exclude that proportions of capelin spawning in summer may vary with changes in environmental conditions, as the climate effect on recruitment may differ between spawning seasons.

4.5 Recommendations to future research to improve understanding of variation in spawning time

It is apparent from this study that IMR has not have focussed on summer spawning capelin, as this is out of the main fishing season in spring one has to have special sampling plans and own surveys to study the summer spawners and their eggs and larvae in more detail to understand more about the early life stages. Acoustic surveys could have revealed more about abundance during this spawning season.

It is possible to study the otolith microstructure in more details, compare daily otolith growth in grinded otoliths of spring and summer spawners, as done in several herring studies. This could be interesting with regard to survival.

Moreover, genetic methods have evolved greatly in recent years, and it may be possible that such effort would make it possible to better split between spring and summer spawners mixing during feeding season. It could perhaps give further insight into the actual proportions of summer spawners. However, there are also other more easy analyses that can be carried out on the otolith material, such as otolith shape analyses (Burke *et al*., 2008), analysis of otolith microstructure (Clausen *et al*., 2007) and new technologies in genetics like analysis on Single Nucleotide Polymorphism (SNPs) (Lamichhanney *et al*., 2012; Limborg *et al.,* 2012) that is also used to split between fish populations, and especially between spawning seasons.

REFERENCES

Aneer, G. 1985. Some speculations about the Baltic herring (*Clupea Harengus membras* L.) in connection with the eutrophication of the Baltic Sea. Canadian Journal Fisheries and Aquatic Sciences, 42: 83-90.

Bakanev, V. S., and Sergeeva, T. M. 1994. Results of acoustic survey for capelin (*Mallotus villosus*) in NAFO divisions 3LNO in 1993. NAFO SCR Document 94/14, Serial No. N2377. 5 pp.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. Progress in Oceanography, 68: 271–288.

Barbaro, A., Einarsson, B., Birnir, B., Sigurðsson, S., Valdimarsson, H., Palsson, O. K., Sveinbjornsson, S., and Sigurðsson, T. 2009. Modelling and simulations of the migration of pelagic fish. ICES Journal of Marine Science, 66: 826-838.

Bernardo, J. 1993. Determinants of maturation in animals. Trends in Ecology and Evolution, 8:166–173.

Bjørke, H., Fossum, P., and Sætre, R. 1986. Distribution, drift and condition of herring larvae off western Norway in 1985. ICES Documents CM 1986/H: 39. 25pp.

Bogstad, B., Dingsør, G. E., Ingvaldsen, R. B. and Gjøsæter, H. 2013. Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. Marine Biology Research, 9: 895-907.

Brett, J. R. 1979. Environmental factors and growth. *In* Fish Physiology, Vol. VIII: Bioenergetics and Growth, pp. 599-675. Ed. by V. S. Hoar, D. J. Randall and J. R. Brett. Academic Press, New York.

Brophy, D., Danilowicz, B. S., and King, P. A. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 63: 607-616.

Brophy, D., and Danilowicz, B. S. 2003. The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus* L.). ICES Journal of Marine Science, 60: 1103–1113.

Browman, H. I. 2000. Application of evolutionary theory to fisheries science and stock assessment-management. Marine Ecology Progress Series, 208: 299.

Burke, N., Brophy, D., and King, P. 2008. Shape analysis of otolith annuli in Atlantic herring (*Clupea harengus*); a new method for tracking fish populations. Fisheries Research, 91: 133-143.

Campana, S. E., and Neilson, J. D. 1985. Microstructure of fish otoliths. Canadian. Journal of Fisheries and Aquatic Science, 42: 1014-1032.

Carscadden, J., and Nakashima, B. S. 1997. Abundance and changes in distribution, biology, and behavior of capelin in response to cooler waters of the 1990s. *In* Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Lowell Wakefield Fisheries Symposium Series no. 14, pp. 457-468. American Fisheries Society, Fairbanks, AK.

Christiansen, J. S., Præbel, K., and Siikavuopio, S. I. 2008. Facultative semelparity in capelin *Mallotus villosus*(Osmeridae)—an experimental test of a life history phenomenon in a sub-arctic fish. Journal of Experimental Marine Biology and Ecology, 360:47-55.

Clausen, L. A. W., Bekkevold, D., Hatfield, E. M. C. and Moseggard, M. 2007. Application and validation of otolith microstructure as a stock identification method in mixed Atlantic herring (*Clupea harengus*) stock in the North Sea and the Western Baltic. ICES Journal of Marine Science, 64: 377-385.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. Journal du Conseil International pour l'Exploration de la Mer, 33: 81–97.

Dalpadado, P., Ingvaldsen, R. B., Stige, L. C., Bogstad, B., Knutsen, T., Ottersen, G., and Ellertsen, B. 2012. Climate effects on Barents Sea ecosystem dynamics. ICES Journal of Marine Science, 69:1303-1316.

Davoren, G. K., Penton, P., Burke, C., and Montevecchi, W. A. 2012. Water temperature and timing of capelin spawning determine seabird diets. ICES Journal of Marine Science, 69:1234-1241.

Drevetnyak, K. V., Antsiferov, M. Y. and Murashko, P. A. 2011. The effect of climate fluctuations on demersal fisheries in the Barents Sea and adjacent waters. Climate change and effects on the Barents Sea marine living resources: IMR/PINRO Joint Report Series 2/2011. 105-113pp.

Eklund, J., Rajasilta, M. and Laine, P. 2001. Growth pattern of Baltic herring in relation to spawning time. Herring: expectation for the new millennium: Alaska Sea Grant College Program 2001/AK-SG-01-04. 55-170pp.

Flynn, S. R., and Burton, M. P. M. 2003. Gametogenesis in capelin, *Mallotus villosus* (Muller), in the Northwest Atlantic Ocean. Canadian Journal of Zoology, 81: 1511–1523.

Folkvord, A., Johannesen, A., and Moksness, E. 2004. Temperature dependent otolith growth in Norwegian spring spawning herring (*Clupea harengus* L.) larvae. Sarsia, 89: 297–310.

Gjøsæter, H. 1986. Growth of the Barents Sea capelin compared to stock size and geographical distribution. ICES Document CM 1986/H: 38. 16 pp.

Gjøsæter, H. 1995. Pelagic fish and ecological impact of modern fishing industry in the Barents Sea. Arctic, 48: 267-278.

Gjøsæter, H. 1998. The population biology and exploitation of capelin *(Mallotus villosus)* in the Barents Sea. Sarsia, 83:453-496.

Gjøsæter, H. 1999. Studies on the Barents Sea capelin (*Mallotus villosus* Muller), with emphasis on growth. PhD thesis, Department of Biology, University of Bergen.160 pp.

Gjøsæter, H., and Bogstad, B. 1998. Effects of the presence of herring (*Clupea harengus*) on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). Fisheries Research, 38: 57-71.

Gjøsæter, H., and Loeng, H. 1984. Distribution and growth of capelin in Barents Sea in relation to water temperature in the period 1974-1983. ICES Document CM 1984/ Gen: 16/Mini-symp.16 pp.

Gjøsæter, H., and Loeng, H. 1987. Growth of the Barents Sea Capelin, *Mallotus villosus*, in relation to climate. Environmental Biology of Fisheries, 20: 293-300.

Gjøsæter, H., Dalpadado, P., and Hassel, A. 2002.Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. ICES Journal of Marine Science, 59: 959-67.

Gjøsæter, H., Ushakov, N. G., Prozorkevich, D. V. 2011. Capelin. *In* The Barents Sea: Ecosystem, Resources, Management: Half a Century of Russian- Norwegian Cooperation, pp. 201-214. Ed. by T. Jakobsen and V.K. Ozhigin. Tapir Akademisk Forlag, Trondheim, Norway.

Haegele, C.W., and Schweigert, J. F. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behaviour. Canadian Journal of Fisheries and Aquatic Sciences, 42: 39-55.

Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences, 42: 111–126.

Hay, D. E., and Brett, J. R. 1985. Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): an experimental study with comparisons to natural populations. Canadian Journal of Fisheries and Aquatic Sciences, 45: 399-406.

Heino, M., and Godø, O. R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639–656.

Heino, M., Dieckmann, U., and Godø, O. R. 2002. Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Holst, J. C., and Slotte, A. 1998. Effects of juvenile nursery on geographic spawning distribution in Norwegian spring-spawning herring *(Clupea harengus* L.). ICES Journal of Marine Science, 55: 987–996.

Huse, G., and Toresen, R. 1995. Predation by juvenile herring (*Clupea harengus* L.) on Barents Sea capelin (*Mallotus villosus* Muller) larvae. *In* Precision and relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea and adjacent waters. Proceedings of the sixth IMRPINRO symposium, Bergen, 14-17 June 1994, pp. 59-73. Institute of Marine Research, Bergen, Norway.

Husebø, Å., Slotte, A., and Folkvord, A. 2005. Growth differences in juvenile Norwegian spring spawning herring (*Clupea harengus* L.) related to temperature conditions in the nursery areas. ICES Document CM 2005/O: 07.

Husebø, A., Slotte, A., and Stenevik, E. K. 2007. Growth of juvenile Norwegian spring-spawning herring in relation to latitudinal and interannual differences in temperature and fish density in their coastal and fjord nursery areas. ICES Journal of Marine Science, 64: 1161–1172.

Husebø, Å., Stenevik, E. K., Slotte, A., Fossum, P., Salthaug, A., Vikebø, F., Aanes, S., and Folkvord, A. 2009. Effects of hatching time on year-class strength in Norwegian spring pawning herring (*Clupea harengus*). ICES Journal of Marine Science, 66: 1710–1717.

Hutchings, J. A., and Myers, R. A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, Gadus morhua, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 50: 2468-2474.

ICES. 2000. Report of the Northern pelagic and blue whiting fisheries working group. ICES Document CM 2000/ACFM: 16. 170pp.

ICES. 2011. Report of the Arctic Fisheries Working Group, Hamburg, 28 April–4 May 2011. ICES Document CM 2011/ACOM: 05. 659pp.

Ingvaldsen, R., Loeng, H., Ottersen, G., and Ådlandsvik, B. 2003 Climate variability in the Barents Sea during the 20th century with a focus on the 1990s. ICES Marine Science Symposia, 219: 160–168.

Ivarjord, T., Pedersen, T., and Moksness, E. 2008. Effects of growth rates on the otolith increments deposition rate in Capelin larvae (*Mallotus villosus*). Journal of Experimental Marine Biology and Ecology, 358: 170-177.

Jobling, M. 1994. Fish Bioenergetics. Chapman & Hall, London. 309pp.

Karino, K., and Kuwamura, T. 1997. Plasticity in spawning visits of female damselfish, Stegastes nigricans: effect of distance to mates. Behavioral Ecology and Sociobiology, 41: 55-59.

Kjesbu, O. S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. Journal of Fish Biology, 45: 719-735.

Laine, P. and Rajasilta, M. 1998. Changes in the reproductive properties of Baltic herring females during the spawning season. Fisheries Research, 36: 67-73.

Lamichhaney, S., Barrio, A.M., Rafati, N., G. Sundström, C. J. Rubin, E. R. Gilbert, J. Berglund, A. Wetterbom, L. Laikre, M. T. Webster, M. Grabherr, N. Rymann, and Andersson, L. 2012. Population- scale sequencing reveals genetic differentiation due to local adaptation in Atlantic herring. Proceedings of the National Academy of Sciences, 109:19345-19350.

Lavigne, D. M. 1996. Ecological interactions between marine mammals, commercial fisheries and their prey: unraveling the tangled web. *In* High-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. W.A. Montevecchi (ed.). Canadian Wildlife Service Occasional Paper 91: 59–71.

Law, R., 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659–668.

Lilly, G. R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and northeast Newfound-land shelves during a period of changing spatial distributions. ICES Marine Science Symposia, 198: 600–611.

Limborg, M. T., Helyar, S. J., Bruyn, M. D., Taylor, M. I., Nielsen, E. E., Ogden, R. O. B., Carvalho, G. R., Consortium, F. P. T. and Bekkevold. M. 2012. Environmental selection on transcriptome –derived SNPs in high gene flow in marine fish, the Atlantic herring *(Clupea harengus)*. Molecular Ecology, 21: 3686-3703.

Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. Polar Research, 10: 5-18.

Loeng, H., Ozhigin, V., and Ådlandsvik, B. 1997. Water fluxes through the Barents Sea. ICES Journal of Marine Science, 54: 310–317.

Marteinsdottir, G., and Björnsson, H. 1999. Time and duration of spawning of cod in Icelandic waters. ICES Document CM 1999/Y: 34. 22pp.

Miller, D. S. 1994. Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 2J3KL in the autumn of 1993, p. 91-98. *In* Capelin in SA2 + Div. 3KL. Ed.by J. Carscadden. DFO Atlantic Fisheries Research Document 94/18.

Mjanger, H., Hestenes, K., Svendsen, E. O. B. V., Wenneck, T. D. L. 2006. Manual for sampling of fish and crustaceans. IMR, Bergen. 115pp.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science, 62: 1270–1280.

Nakashima, B.S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). NAFO Scientific Council Studies, 24:55-68.

Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A.,and Gjøsæter, H. 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES Journal of Marine Science, 67: 87-101.

Orlova, E. L, Botisov, V. D, Dolgov, A. V, Rudneva, G. B, and Nesterova, V. N. 2005. The relationship between plankton, capelin, and cod under different temperature conditions. ICES Journal of Marine Science, 62:1281-92.

Orlova, E. L., Boitsov, V.D., and Nesterova, V. N. 2010.The Influence of Hydrographic Conditions on the Structure and Functioning of the Trophic Complex Plankton Pelagic Fishes Cod. Murmansk: Polar Research Institute of Marine Fisheries and Oceanography (PINRO). 190 pp.

Ottersen, G., and Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES Journal of Marine Science, 57: 339–348.

Prokhorov, V. S. 1968. Materials on the ecology of capelin in the Barents Sea. Rapports et procès-verbaux des réunions / Conseil permanent international pour l'exploration de la mer, 158: 23-31.

R Development Core Team. 2006. R: a language and environment for statistical computing (version 2.3.1). R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rajasilta, M. 1992. Relationship between food, fat, sexual maturation, and spawning time of Baltic herring (*Clupea harengus membras*) in the archipelago sea. Canadian Journal of Fisheries and Aquatic Sciences, 49:644–654.

Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea "canary" for marine ecosystem change. ICES Journal of Marine Science, 62: 1524-1530.

Sakshaug, E. and Kovacs, K. 2009. Introduction. *In* Ecosystem Barents Sea, pp. 9-32. Ed. by E. Sakshaug, G. Johnsen, G. and K. Kovacs. Tapir Academic Press, Trondheim.

Shackell, N.L., Carscadden, J.E., and Miller, D.S. 1994. Migration of pre-spawning capelin (*Mallotus villosus*) are related to temperature on the northern Grand Bank, Newfoundland. ICES Journal of Marine Science, 51:107-114.

Skjoldal, H. R., Gjøsæter H., and Loeng, H. 1992. The Barents Sea ecosystem in the 1980s: ocean climate, plankton, and capelin growth. ICES Marine Science Symposia, 195: 278-290.

Slotte, A. 1999. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia, 84: 111–127.

Slotte, A., Johannessen, A., and Kjesbu O. S. 2000. Effects of fish size on spawning time in Norwegian spring-spawning herring. Journal of Fish Biology, 56: 295–310.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, New York.

Templeman, W. 1948.The life history of the capelin (*Mallotus villosus* O.F. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory, 17: 1–151.

Vandeperre, F., and Methven, D. 2007. Do bigger fish arrive and spawn at the spawning grounds before smaller fish: cod (*Gadus morhua*) predation on beach spawning capelin *(Mallotus villosus*) from coastal Newfoundland. Estuarine, Coastal and Shelf Science, 71: 391–400.

Vikebø, F., Husebø, Å, Slotte, A., Stenevik, E., and Lien, V. 2010. Effect of hatching date, vertical distribution, and interannual variation in physical forcing on northward displacement and temperature conditions of Norwegian spring-spawning herring larvae. ICES Journal of Marine Science, 67: 1948-1956.

Vikebø, F., Jørgensen, C., Kristiansen, T., and Fiksen, Ø. 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Marine Ecology Progress Series, 347: 207–219.

Ware, D. M., and Tanasichuk, R. W. 1989. Biological basis of maturation and spawning waves in Pacific herring *Clupea harengus pallasi*. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1776–1784.

Watanabe, C., and Yatsu, A. 2004. Effects of density-dependence and sea surface temperature on interannual variation in length-at-age of chub mackerel (*Scomber japonicus*) in the Kuroshio–Oyashio area during 1970–1997. Fishery Bulletin, 102: 196–206.

Wieland, K., Jarre-Teichmann, A., and Horbowa, K. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science, 57: 452–464.

Zuzarte, F., Köster, F. W., Möllmann, C., Voss, R., and Grønkjær, P. 1996. Diet composition of cod larvae in the Bornholm Basin. ICES CM 1996/J:19.

Table 3: Number of fish in February, March and June in each year. 3-7(mature, spawning and spent) stages fish and statistical areas 1-5 were used.

Year	February	March	June
1976	568	893	0
1977	796	299	221
1978	0	0	0
1979	21	309	1
1980	0	0	0
1981	2918	2945	0
1982	0	98	250
1983	1723	1414	0
1984	1787	2287	729
1985	0	1298	124
1986	0	0	0
1987	0	94	0
1988	0	110	0
1989	96	421	1
1990	34	99	20
1991	1089	1381	27
1992	200	1157	23
1993	0	397	0
1994	333	0	82
1995	38	0	0
1996	100	150	795
1997	142	0	44
1998	0	0	0
1999	156	981	0

2000	516	1174	0
2001	209	700	0
2002	389	1871	0
2003	453	1010	0
2004	600	80	0
2005	150	768	50
2006	250	259	2
2007	253	450	0
2008	1233	490	0
2009	464	822	0
2010	662	879	0
2011	658	723	0
2012	551	748	0

```
Female


> summary(M)

Call:
lm(formula = lengde ~ factor(mnd) * factor(aar), data = s10)

Residuals:
    Min      1Q  Median      3Q     Max
-4.0229 -0.6193 -0.0229  0.6351  3.7865

Coefficients:
                                      Estimate Std. Error t value Pr(>|t|)
(Intercept)                           15.83493    0.03835 412.860  < 2e-16 ***
factor(mnd)summer                     -0.95121    0.08267 -11.507  < 2e-16 ***
factor(aar)1982                       -0.55288    0.15850  -3.488 0.000490 ***
factor(aar)1984                       -0.71562    0.04369 -16.380  < 2e-16 ***
factor(aar)1985                       -0.48795    0.05579  -8.747  < 2e-16 ***
factor(aar)1996                       -0.97006    0.09890  -9.809  < 2e-16 ***
factor(mnd)summer:factor(aar)1982  0.38261    0.18941   2.020 0.043442 *
factor(mnd)summer:factor(aar)1984 -0.14524    0.09542  -1.522 0.128048
factor(mnd)summer:factor(aar)1985 -0.64067    0.16522  -3.878 0.000107 ***
factor(mnd)summer:factor(aar)1996  0.55623    0.12972   4.288 1.84e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.9604 on 4880 degrees of freedom
Multiple R-squared:  0.2195,   Adjusted R-squared:  0.2181
F-statistic: 152.5 on 9 and 4880 DF,  p-value: < 2.2e-16




Male


Call:
lm(formula = lengde ~ factor(mnd) * factor(aar), data = s11)

Residuals:
    Min      1Q  Median      3Q     Max
-3.8761 -0.5852 -0.0852  0.6239  3.3580

Coefficients:
                                      Estimate Std. Error t value Pr(>|t|)
(Intercept)                           17.58226    0.04430 396.888  < 2e-16 ***
factor(mnd)summer                     -1.30675    0.14390  -9.081  < 2e-16 ***
factor(aar)1982                       -0.77718    0.13240  -5.870 4.71e-09 ***
factor(aar)1984                       -0.99707    0.04929 -20.228  < 2e-16 ***
factor(aar)1985                       -0.94028    0.05666 -16.595  < 2e-16 ***
factor(aar)1996                       -1.07507    0.09258 -11.613  < 2e-16 ***
factor(mnd)summer:factor(aar)1982  0.55230    0.21886   2.524 0.011656 *
factor(mnd)summer:factor(aar)1984  0.59766    0.15886   3.762 0.000171 ***
factor(mnd)summer:factor(aar)1985  0.42477    0.18493   2.297 0.021677 *
factor(mnd)summer:factor(aar)1996  0.71656    0.17616   4.068 4.84e-05 ***
---
```

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.9584 on 4034 degrees of freedom
Multiple R-squared:  0.1725,   Adjusted R-squared:  0.1707
F-statistic: 93.46 on 9 and 4034 DF,  p-value: < 2.2e-16
```

Appendix 3

```
Female

> summary(M2)

Call:
lm(formula = vekt ~ factor(mnd) * factor(aar), data = s11)

Residuals:
     Min       1Q   Median       3Q      Max
-10.2941  -2.9841  -0.2941   2.4035  20.9513

Coefficients:
                                 Estimate Std. Error t value Pr(>|t|)
(Intercept)                       18.0487     0.1746 103.376  < 2e-16 ***
factor(mnd)summer                 -3.1011     0.3587  -8.645  < 2e-16 ***
factor(aar)1982                    1.1051     0.6808   1.623  0.10460
factor(aar)1984                   -1.7546     0.1962  -8.943  < 2e-16 ***
factor(aar)1985                    0.6826     0.2460   2.774  0.00555 **
factor(aar)1996                   -3.6613     0.4273  -8.568  < 2e-16 ***
factor(mnd)summer:factor(aar)1982 -1.4563     0.8127  -1.792  0.07320 .
factor(mnd)summer:factor(aar)1984 -0.2090     0.4126  -0.506  0.61258
factor(mnd)summer:factor(aar)1985 -3.6303     0.7095  -5.117 3.23e-07 ***
factor(mnd)summer:factor(aar)1996  3.1662     0.5582   5.672 1.50e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 4.109 on 4807 degrees of freedom
Multiple R-squared:  0.1521,   Adjusted R-squared:  0.1505
F-statistic: 95.81 on 9 and 4807 DF,  p-value: < 2.2e-16


Male

> summary(M3)

Call:
lm(formula = vekt ~ factor(mnd) * factor(aar), data = s12)

Residuals:
     Min       1Q   Median       3Q      Max
-15.9433  -3.5585  -0.5585   3.4415  21.0567

Coefficients:
                                 Estimate Std. Error t value Pr(>|t|)
(Intercept)                      27.943311   0.256468 108.954  < 2e-16 ***
factor(mnd)summer                -6.208617   0.811023  -7.655 2.40e-14 ***
factor(aar)1982                   0.988893   0.746607   1.325   0.1854
factor(aar)1984                  -2.384816   0.283778  -8.404  < 2e-16 ***
```

```
factor(aar)1985                         -1.709615   0.324326  -5.271 1.43e-07 ***
factor(aar)1996                         -6.698706   0.523889 -12.786  < 2e-16 ***
factor(mnd)summer:factor(aar)1982 -1.356498   1.231496  -1.102   0.2707
factor(mnd)summer:factor(aar)1984  1.747468   0.894909   1.953   0.0509 .
factor(mnd)summer:factor(aar)1985  0.001588   1.041120   0.002   0.9988
factor(mnd)summer:factor(aar)1996  6.385065   0.991907   6.437 1.36e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 5.386 on 4007 degrees of freedom
Multiple R-squared:  0.1367,   Adjusted R-squared:  0.1348
F-statistic: 70.51 on 9 and 4007 DF,  p-value: < 2.2e-16
```

Appendix 4

```
Female

Kruskal-Wallis rank sum test

data:  alder by mnd
Kruskal-Wallis chi-squared = 1319.172, df = 1, p-value < 2.2e-16


Male

Kruskal-Wallis rank sum test

data:  alder by mnd
Kruskal-Wallis chi-squared = 620.4199, df = 1, p-value < 2.2e-16
```

Appendix 5

```
Female
Call:
lm(formula = lengde ~ factor(mnd) + alder + factor(aar) + factor(mnd):factor(
aar),
    data = samina13)

Residuals:
    Min      1Q  Median      3Q     Max
-3.2073 -0.6731 -0.0855  0.6171  3.6171

Coefficients:
                                Estimate Std. Error t value Pr(>|t|)
(Intercept)                     14.67686    0.14289 102.718  < 2e-16 ***
factor(mnd)summer               -0.81274    0.09805  -8.289  < 2e-16 ***
alder                            0.29017    0.03439   8.437  < 2e-16 ***
```

```
factor(aar)1982                          -0.53666     0.16378   -3.277 0.001060  **
factor(aar)1984                          -0.66446     0.05360  -12.396  < 2e-16  ***
factor(aar)1985                          -0.39562     0.06400   -6.182 6.98e-10 ***
factor(aar)1996                          -0.58615     0.11293   -5.190 2.21e-07 ***
factor(mnd)summer:factor(aar)1982  1.00932     0.20385    4.951 7.69e-07 ***
factor(mnd)summer:factor(aar)1984 -0.02987     0.10903   -0.274 0.784160
factor(mnd)summer:factor(aar)1985 -0.58339     0.17250   -3.382 0.000727 ***
factor(mnd)summer:factor(aar)1996  0.93700     0.16080    5.827 6.09e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.924 on 3912 degrees of freedom
Multiple R-squared:  0.1986,   Adjusted R-squared:  0.1966
F-statistic: 96.95 on 10 and 3912 DF,  p-value: < 2.2e-16


Male


Call:
lm(formula = lengde ~ factor(mnd) + alder + factor(aar) + alder:factor(aar) +

    factor(mnd):factor(aar), data = samina14)

Residuals:
    Min      1Q  Median      3Q     Max
-3.8043 -0.5730 -0.0730  0.5939  3.2424

Coefficients:
                                   Estimate Std. Error t value Pr(>|t|)
(Intercept)                        15.09537    0.80237  18.813  < 2e-16  ***
factor(mnd)summer                  -1.13218    0.18209   -6.218 5.68e-10 ***
alder                               0.61074    0.20324    3.005 0.002676 **
factor(aar)1982                     1.46345    1.10850    1.320 0.186860
factor(aar)1984                     1.02087    0.82503    1.237 0.216041
factor(aar)1985                     0.01082    0.84877    0.013 0.989833
factor(aar)1996                    -0.01702    0.95524   -0.018 0.985788
alder:factor(aar)1982              -0.56783    0.28762   -1.974 0.048440 *
alder:factor(aar)1984              -0.49653    0.20938   -2.371 0.017778 *
alder:factor(aar)1985              -0.19788    0.21648   -0.914 0.360722
alder:factor(aar)1996              -0.17066    0.25180   -0.678 0.497969
factor(mnd)summer:factor(aar)1982  1.33301    0.27226    4.896 1.03e-06 ***
factor(mnd)summer:factor(aar)1984  0.47764    0.19501    2.449 0.014366 *
factor(mnd)summer:factor(aar)1985  0.49638    0.22450    2.211 0.027101 *
factor(mnd)summer:factor(aar)1996  0.91325    0.23811    3.835 0.000128 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.9416 on 3267 degrees of freedom
Multiple R-squared:  0.1258,   Adjusted R-squared:  0.122
F-statistic: 33.57 on 14 and 3267 DF,  p-value: < 2.2e-16
```

```
Female
Call:
lm(formula = vs1mm ~ factor(mnd) + alder + aar, data = samina13)

Residuals:
      Min        1Q    Median        3Q       Max
-0.155289 -0.036502  0.004362  0.035644  0.309740

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)  10.9172831  0.4292399   25.43   <2e-16 ***
factor(mnd)2 -0.0312830  0.0021242  -14.73   <2e-16 ***
alder        -0.0393619  0.0015474  -25.44   <2e-16 ***
aar          -0.0053040  0.0002148  -24.69   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05489 on 4100 degrees of freedom
Multiple R-squared:  0.1801,   Adjusted R-squared:  0.1795
F-statistic: 300.2 on 3 and 4100 DF,  p-value: < 2.2e-16


>


Male
Call:
lm(formula = vs1mm ~ factor(mnd) + alder + aar + factor(mnd):alder +
    alder:aar + factor(mnd):aar + factor(mnd):alder:aar, data = samina14)

Residuals:
      Min        1Q    Median        3Q       Max
-0.165853 -0.037922 -0.005265  0.037819  0.251234

Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)            2.910e+01  4.348e+00   6.693 2.56e-11 ***
factor(mnd)2          -2.681e+01  5.090e+00  -5.267 1.47e-07 ***
alder                 -4.679e+00  1.149e+00  -4.071 4.79e-05 ***
aar                   -1.447e-02  2.191e-03  -6.605 4.63e-11 ***
factor(mnd)2:alder     7.832e+00  1.490e+00   5.257 1.56e-07 ***
alder:aar              2.341e-03  5.793e-04   4.041 5.45e-05 ***
factor(mnd)2:aar       1.351e-02  2.563e-03   5.269 1.46e-07 ***
factor(mnd)2:alder:aar -3.951e-03 7.506e-04  -5.263 1.51e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05643 on 3277 degrees of freedom
Multiple R-squared:  0.1647,   Adjusted R-squared:  0.1629
F-statistic: 92.31 on 7 and 3277 DF,  p-value: < 2.2e-16
```

```
Age 3
Call:
lm(formula = vs1mm ~ lengde + factor(mnd) + lengde:factor(mnd),
    data = samina14)

Residuals:
     Min       1Q   Median       3Q      Max
-0.17350 -0.04466  0.00203  0.04891  0.35130

Coefficients:
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)               0.129880   0.021938   5.920 3.71e-09 ***
lengde                    0.009183   0.001401   6.556 6.86e-11 ***
factor(mnd)summer         0.097940   0.034954   2.802 0.005123 **
lengde:factor(mnd)summer -0.008406   0.002312  -3.636 0.000283 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.06423 on 2226 degrees of freedom
Multiple R-squared:  0.07909,   Adjusted R-squared:  0.07784
F-statistic: 63.72 on 3 and 2226 DF,  p-value: < 2.2e-16


Age 4
Call:
lm(formula = vs1mm ~ lengde + factor(mnd) + lengde:factor(mnd),
    data = samina15)

Residuals:
      Min        1Q    Median        3Q       Max
-0.164437 -0.038064  0.003291  0.034225  0.178803

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)
(Intercept)               0.0546218  0.0125099   4.366  1.3e-05 ***
lengde                    0.0117829  0.0007837  15.035  < 2e-16 ***
factor(mnd)summer         0.0717424  0.0389451   1.842   0.0655 .
lengde:factor(mnd)summer -0.0061563  0.0025018  -2.461   0.0139 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Call:
glm(formula = vs1mm ~ factor(mnd) + factor(alder) + lengde, data = samina13)

Deviance Residuals:
      Min          1Q      Median          3Q         Max
-0.162026  -0.032626  -0.000941   0.034453   0.167734

Coefficients:
                     Estimate Std. Error t value Pr(>|t|)
(Intercept)          0.1048122  0.0107606   9.740  < 2e-16 ***
factor(mnd)summer   -0.0181563  0.0024544  -7.397 1.67e-13 ***
factor(alder)4      -0.0334803  0.0018955 -17.663  < 2e-16 ***
lengde               0.0110047  0.0006882  15.990  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.002732185)

    Null deviance: 12.743  on 4128  degrees of freedom
Residual deviance: 11.270  on 4125  degrees of freedom
AIC: -12648

Number of Fisher Scoring iterations: 2
```

```
Female

Call:
lm(formula = df ~ factor(mnd) + alder + aar + factor(mnd):alder +
    alder:aar + factor(mnd):aar, data = samina14)

Residuals:
     Min       1Q   Median       3Q      Max
-0.26663 -0.04874 -0.00427  0.04575  0.41750

Coefficients:
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)             32.2710619  2.3910475  13.497  < 2e-16 ***
factor(mnd)summer       -4.5975667  1.3944914  -3.297 0.000986 ***
alder                   -5.8880956  0.5984560  -9.839  < 2e-16 ***
aar                     -0.0160335  0.0012041 -13.316  < 2e-16 ***
factor(mnd)summer:alder  0.0068900  0.0042451   1.623 0.104653
alder:aar                0.0029703  0.0003016   9.849  < 2e-16 ***
factor(mnd)summer:aar    0.0022807  0.0006998   3.259 0.001127 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07398 on 4097 degrees of freedom
Multiple R-squared:  0.3297,   Adjusted R-squared:  0.3287
F-statistic: 335.8 on 6 and 4097 DF,  p-value: < 2.2e-16
```

```
Male

Call:
lm(formula = df ~ factor(mnd) + alder + aar + factor(mnd):alder +
    alder:aar + factor(mnd):aar, data = samina15)

Residuals:
     Min       1Q   Median       3Q      Max
-0.31846 -0.04988 -0.00148  0.04786  0.45983

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)
(Intercept)              38.0014151  3.8634349   9.836  < 2e-16 ***
factor(mnd)summer        -8.9449535  1.9881426  -4.499 7.06e-06 ***
alder                    -6.5236785  0.9974873  -6.540 7.10e-11 ***
aar                      -0.0189144  0.0019466  -9.717  < 2e-16 ***
factor(mnd)summer:alder   0.0117337  0.0053807   2.181   0.0293 *
alder:aar                 0.0032885  0.0005027   6.542 7.03e-11 ***
factor(mnd)summer:aar     0.0044648  0.0009986   4.471 8.04e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.077 on 3278 degrees of freedom
Multiple R-squared:  0.2313,   Adjusted R-squared:  0.2299
F-statistic: 164.4 on 6 and 3278 DF,  p-value: < 2.2e-16
```

Appendix 10

```
Age 3

Call:
lm(formula = df ~ lengde + factor(mnd), data = samina14)

Residuals:
     Min       1Q   Median       3Q      Max
-0.26251 -0.04985 -0.00133  0.04766  0.47810

Coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)       0.4710892  0.0208356  22.610   <2e-16 ***
lengde           -0.0007306  0.0013279  -0.550    0.582
factor(mnd)summer -0.0313217  0.0035213  -8.895   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07653 on 2227 degrees of freedom
Multiple R-squared:  0.0369,   Adjusted R-squared:  0.03604
F-statistic: 42.66 on 2 and 2227 DF,  p-value: < 2.2e-16
```

```
Age 4
Call:
lm(formula = df ~ factor(mnd), data = samina15)

Residuals:
     Min       1Q    Median       3Q      Max
-0.32212 -0.05355 -0.00212  0.04729  0.31788

Coefficients:
                    Estimate Std. Error t value Pr(>|t|)
(Intercept)         0.482117   0.001316  366.41   <2e-16 ***
factor(mnd)summer  -0.055332   0.004152  -13.33   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07885 on 3990 degrees of freedom
Multiple R-squared:  0.04262,   Adjusted R-squared:  0.04238
F-statistic: 177.6 on 1 and 3990 DF,  p-value: < 2.2e-16
```

Appendix 11

```
Call:
glm(formula = df ~ factor(mnd) * factor(alder) + lengde, data = samina14)

Deviance Residuals:
     Min        1Q     Median        3Q       Max
-0.33487  -0.04822   0.00513    0.04593   0.48518

Coefficients:
                                  Estimate Std. Error t value Pr(>|t|)
(Intercept)                      0.4423661  0.0146643  30.166  < 2e-16 ***
factor(mnd)summer               -0.0220705  0.0041097  -5.370 8.29e-08 ***
factor(alder)4                   0.0419223  0.0027970  14.988  < 2e-16 ***
lengde                           0.0006223  0.0009320   0.668   0.5044
factor(mnd)summer:factor(alder)4 -0.0165480  0.0067372  -2.456   0.0141 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.004978163)

    Null deviance: 23.042  on 4128  degrees of freedom
Residual deviance: 20.530  on 4124  degrees of freedom
AIC: -10170

Number of Fisher Scoring iterations: 2
```

```
Call:
glm(formula = vekt ~ lengde * aar * factor(kjonn) + factor(mnd),
    data = samina12)

Deviance Residuals:
     Min       1Q   Median       3Q      Max
-12.8262  -1.8082   0.0401   1.6686  16.8951

Coefficients:
                            Estimate Std. Error t value Pr(>|t|)
(Intercept)                -9.668e+02  2.246e+02  -4.304 1.70e-05 ***
lengde                      6.059e+01  1.507e+01   4.021 5.84e-05 ***
aar                         4.706e-01  1.132e-01   4.157 3.25e-05 ***
factor(kjonn)2              1.788e+03  3.927e+02   4.554 5.34e-06 ***
factor(mnd)summer          -5.393e-01  8.011e-02  -6.733 1.77e-11 ***
lengde:aar                 -2.888e-02  7.594e-03  -3.804 0.000144 ***
lengde:factor(kjonn)2      -1.086e+02  2.460e+01  -4.412 1.04e-05 ***
aar:factor(kjonn)2         -9.111e-01  1.979e-01  -4.604 4.21e-06 ***
lengde:aar:factor(kjonn)2   5.543e-02  1.240e-02   4.469 7.95e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 7.818985)

    Null deviance: 400390  on 8670  degrees of freedom
Residual deviance:  67728  on 8662  degrees of freedom
AIC: 42451

Number of Fisher Scoring iterations: 2
```

```
Call:
lm(formula = vs1mm ~ longN + factor(alder) + factor(LatSep) +
    longN:factor(alder) + longN:factor(LatSep) + factor(alder):factor(LatSep)
 +
    longN:factor(alder):factor(LatSep), data = samina7)

Residuals:
     Min       1Q   Median       3Q      Max
-0.21679 -0.04083  0.00002  0.03936  0.41665

Coefficients:
                                Estimate Std. Error t value Pr(>|t|)

(Intercept)                     3.317e-01  1.655e-03 200.437  < 2e-16 ***
```

```
longN                                      -2.100e-03  4.772e-05 -44.007  < 2e-16 ***
factor(alder)2                             -9.037e-02  2.282e-03 -39.601  < 2e-16 ***
factor(alder)3                             -1.013e-01  3.033e-03 -33.401  < 2e-16 ***
factor(alder)4                             -1.119e-01  8.323e-03 -13.440  < 2e-16 ***
factor(LatSep)b                            -1.171e-02  2.562e-03  -4.572 4.83e-06 ***
longN:factor(alder)2                        1.901e-03  6.462e-05  29.414  < 2e-16 ***
longN:factor(alder)3                        2.086e-03  8.130e-05  25.665  < 2e-16 ***
longN:factor(alder)4                        1.822e-03  2.035e-04   8.956  < 2e-16 ***
longN:factor(LatSep)b                       1.100e-03  7.977e-05  13.789  < 2e-16 ***
factor(alder)2:factor(LatSep)b              4.834e-02  3.210e-03  15.057  < 2e-16 ***
factor(alder)3:factor(LatSep)b              1.676e-02  4.067e-03   4.121 3.78e-05 ***
factor(alder)4:factor(LatSep)b             -3.144e-03  1.062e-02  -0.296  0.76720
longN:factor(alder)2:factor(LatSep)b -1.599e-03 9.669e-05 -16.537 < 2e-16 ***
longN:factor(alder)3:factor(LatSep)b -1.175e-03 1.164e-04 -10.089 < 2e-16 ***
longN:factor(alder)4:factor(LatSep)b -7.237e-04  2.719e-04  -2.661 0.00778 **


---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.0595 on 130637 degrees of freedom
Multiple R-squared:  0.102,    Adjusted R-squared:  0.1019
F-statistic: 989.1 on 15 and 130637 DF,  p-value: < 2.2e-16
```

Appendix 14

```
Age 1 and 2

Welch Two Sample t-test

data:  vs1mm by factor(LatSep)
t = -40.2499, df = 102354.1, p-value < 2.2e-16
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 -0.01639716 -0.01487437
sample estimates:
mean in group a mean in group b
      0.2475124       0.2631482
```

Appendix 15

```
South Area and Age 1

Call:
lm(formula = vs1mm ~ longN, data = samina11)

Residuals:
     Min       1Q    Median       3Q      Max
-0.216789 -0.037124 -0.003992  0.036266  0.286524
```

```
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3.317e-01  1.501e-03  220.92   <2e-16 ***
longN       -2.100e-03  4.329e-05  -48.51   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05398 on 24952 degrees of freedom
Multiple R-squared:  0.08617,   Adjusted R-squared:  0.08613
F-statistic:  2353 on 1 and 24952 DF,  p-value: < 2.2e-16


Northern Area and Age 1

Call:
lm(formula = vs1mm ~ longN, data = samina11a)

Residuals:
      Min        1Q     Median        3Q       Max
-0.194858 -0.040975  0.000181  0.038024  0.301026

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  3.200e-01  1.809e-03  176.86   <2e-16 ***
longN       -9.999e-04  5.913e-05  -16.91   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05503 on 12179 degrees of freedom
Multiple R-squared:  0.02294,   Adjusted R-squared:  0.02286
F-statistic: 285.9 on 1 and 12179 DF,  p-value: < 2.2e-16


>
Southern Area and age 2

Call:
lm(formula = vs1mm ~ longN, data = samina12)

Residuals:
     Min       1Q    Median       3Q       Max
-0.16365 -0.04387  0.00462  0.05093  0.41665

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.413e-01  1.719e-03 140.376  < 2e-16 ***
longN       -1.991e-04  4.767e-05  -4.176 2.97e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.06509 on 25132 degrees of freedom
Multiple R-squared:  0.0006936,     Adjusted R-squared:  0.0006538
F-statistic: 17.44 on 1 and 25132 DF,  p-value: 2.971e-05


Northern Area and age 2

Call:
```

```
lm(formula = vs1mm ~ longN, data = samina12a)

Residuals:
     Min       1Q   Median       3Q      Max
-0.17248 -0.04083 -0.00417  0.04123  0.39789

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.779e-01  1.160e-03  239.61   <2e-16 ***
longN       -6.980e-04  3.388e-05  -20.61   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.06116 on 40378 degrees of freedom
Multiple R-squared:  0.01041,	Adjusted R-squared:  0.01038
F-statistic: 424.6 on 1 and 40378 DF,  p-value: < 2.2e-16
```

Southern Area and Age 3

```
Call:
lm(formula = vs1mm ~ longN, data = samina8)

Residuals:
      Min        1Q    Median        3Q       Max
-0.133659 -0.037354  0.001047  0.035258  0.294141

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.304e-01  2.544e-03  90.552   <2e-16 ***
longN       -1.342e-05  6.588e-05  -0.204    0.839
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05955 on 8040 degrees of freedom
Multiple R-squared:  5.163e-06,	Adjusted R-squared:  -0.0001192
F-statistic: 0.04151 on 1 and 8040 DF,  p-value: 0.8386
```

Northern Area and Age 3

```
Call:
lm(formula = vs1mm ~ longN, data = samina8a)

Residuals:
      Min        1Q    Median        3Q       Max
-0.160751 -0.040093  0.007217  0.033256  0.273160

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.354e-01  1.826e-03 128.959   <2e-16 ***
longN       -8.833e-05  5.210e-05  -1.695     0.09 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.0579 on 17376 degrees of freedom
Multiple R-squared:  0.0001654,	Adjusted R-squared:  0.0001079
```

```
F-statistic: 2.875 on 1 and 17376 DF,  p-value: 0.09001




Southern Area and Age 4

Call:
lm(formula = vs1mm ~ longN, data = samina9)

Residuals:
     Min       1Q   Median       3Q      Max
-0.10076 -0.04032 -0.01012  0.03308  0.27627

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.2198241  0.0077102  28.511   <2e-16 ***
longN       -0.0002777  0.0001869  -1.486    0.138
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05624 on 936 degrees of freedom
Multiple R-squared:  0.002353, Adjusted R-squared:  0.001287
F-statistic: 2.207 on 1 and 936 DF,  p-value: 0.1377


Northern Area and Age 4

Call:
lm(formula = vs1mm ~ longN, data = samina9a)

Residuals:
     Min       1Q   Median       3Q      Max
-0.11410 -0.04137 -0.01290  0.03334  0.28962

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) 2.050e-01  6.155e-03  33.301   <2e-16 ***
longN       9.849e-05  1.648e-04   0.598     0.55
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05812 on 1644 degrees of freedom
Multiple R-squared:  0.0002171,      Adjusted R-squared:  -0.000391
F-statistic: 0.3571 on 1 and 1644 DF,  p-value: 0.5502
```

Appendix 16

```
Residuals:
     Min       1Q   Median       3Q      Max
-0.26838 -0.05365 -0.00426  0.05389  0.54280

Coefficients:
```

```
                               Estimate Std. Error t value Pr(>|t|)
(Intercept)                    4.213e-01  1.895e-03 222.353  < 2e-16 ***
longN                          5.289e-06  5.217e-05   0.101 0.919248
factor(alder)3                 3.861e-02  2.618e-03  14.745  < 2e-16 ***
factor(alder)4                 3.834e-02  7.478e-03   5.127 2.95e-07 ***
factor(LatSep)b                2.580e-02  2.174e-03  11.868  < 2e-16 ***
longN:factor(alder)3          -5.159e-04  6.583e-05  -7.837 4.66e-15 ***
longN:factor(alder)4          -4.573e-04  1.754e-04  -2.607 0.009144 **
factor(alder)3:factor(LatSep)b -1.970e-02  1.269e-03 -15.518  < 2e-16 ***
factor(alder)4:factor(LatSep)b -1.766e-02  3.392e-03  -5.205 1.94e-07 ***
longN:factor(LatSep)b         -1.999e-04  6.055e-05  -3.301 0.000963 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07965 on 93508 degrees of freedom
Multiple R-squared:  0.01352,   Adjusted R-squared:  0.01342
F-statistic: 142.3 on 9 and 93508 DF,  p-value: < 2.2e-16
```

Appendix 17

```
Age 2

Welch Two Sample t-test

data:  df by factor(LatSep)
t = -29.9113, df = 51954.97, p-value < 2.2e-16
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 -0.02044570 -0.01793098
sample estimates:
mean in group a mean in group b
      0.4214761       0.4406644


Age 3 and Age 4

Welch Two Sample t-test

data:  df by factor(LatSep)
t = -1.0447, df = 16830.03, p-value = 0.2962
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 -0.0031670120  0.0009648846
sample estimates:
mean in group a mean in group b
      0.4409301       0.4420312
```

Appendix 18

```
Call:
lm(formula = vs1mm ~ year + factor(lon.lat.cat) + factor(kjonn) +
    alder + year:factor(lon.lat.cat) + year:factor(kjonn) + year:alder +
```

```
    factor(lon.lat.cat):factor(kjonn) + factor(lon.lat.cat):alder +
    factor(kjonn):alder + year:factor(lon.lat.cat):alder + year:factor(kjonn)
:alder +
    factor(lon.lat.cat):factor(kjonn):alder, data = df8a)

Residuals:
     Min       1Q   Median       3Q      Max
-0.19912 -0.04097 -0.00134  0.03974  0.42310

Coefficients:
                                 Estimate  Std.Error  t value  Pr(>|t|)
(Intercept)                      3.571e+00  2.020e-01   17.679  < 2e-16 ***
year                            -1.634e-03  1.012e-04  -16.148  < 2e-16 ***
factor(lon.lat.cat)east south   -9.644e-02  3.259e-01   -0.296  0.76726
factor(lon.lat.cat)west north    3.675e-01  3.056e-01    1.203  0.22909
factor(lon.lat.cat)west south   -4.392e+00  3.353e-01  -13.099  < 2e-16 ***
factor(kjonn)2                   4.192e-01  2.263e-01    1.853  0.06395 .
alder                           -1.193e+00  9.410e-02  -12.677  < 2e-16 ***
year:factor(lon.lat.cat)
east south                       4.505e-05  1.633e-04    0.276  0.78272
year:factor(lon.lat.cat)
west north                      -1.951e-04  1.532e-04   -1.274  0.20267
year:factor(lon.lat.cat)
west south                       2.168e-03  1.681e-04   12.894  < 2e-16 ***
year:factor(kjonn)2             -2.103e-04  1.134e-04   -1.854  0.06370 .
year:alder                       5.836e-04  4.718e-05   12.370  < 2e-16 ***
factor(lon.lat.cat)east south:
factor(kjonn)2                   2.208e-03  3.056e-03    0.722  0.47001
factor(lon.lat.cat)west north:
factor(kjonn)2                   3.880e-03  2.746e-03    1.413  0.15758
factor(lon.lat.cat)west south:
factor(kjonn)2                   7.635e-03  2.672e-03    2.858  0.00427 **
factor(lon.lat.cat)east s
outh:alder                      -3.204e-01  1.697e-01   -1.888  0.05897 .
factor(lon.lat.cat)
west north:alder                -1.476e-01  1.395e-01   -1.058  0.29001
factor(lon.lat.cat)
west south:alder                 1.548e+00  1.659e-01    9.330  < 2e-16 ***
factor(kjonn)2:alder            -3.442e-01  1.071e-01   -3.213  0.00132 **
year:factor(lon.lat.cat)
east south:alder                 1.583e-04  8.510e-05    1.860  0.06291 .
year:factor(lon.lat.cat)
west north:alder                 7.733e-05  6.997e-05    1.105  0.26907
year:factor(lon.lat.cat)
west south:alder                -7.651e-04  8.323e-05   -9.193  < 2e-16 ***
year:factor(kjonn)2:alder        1.742e-04  5.372e-05    3.244  0.00118 **
factor(lon.lat.cat)east south:
factor(kjonn)2:alder            -6.019e-04  1.688e-03   -0.357  0.72134
factor(lon.lat.cat)west north:
factor(kjonn)2:alder            -2.932e-03  1.298e-03   -2.259  0.02389 *
factor(lon.lat.cat)west
south:factor(kjonn)2:alder      -4.063e-03  1.435e-03   -2.831  0.00465 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.05959 on 122136 degrees of freedom
Multiple R-squared:  0.09515,  Adjusted R-squared:  0.09496
```

```
F-statistic: 513.7 on 25 and 122136 DF,  p-value: < 2.2e-16
```

```
Call:
lm(formula = dif ~ year + factor(lon.lat.cat) + factor(kjonn) +
    alder + year:factor(lon.lat.cat) + year:factor(kjonn) + year:alder +
    factor(lon.lat.cat):factor(kjonn) + factor(lon.lat.cat):alder +
    factor(kjonn):alder + year:factor(lon.lat.cat):alder + year:factor(kjonn)
:alder,
    data = df9)

Residuals:
     Min       1Q   Median       3Q      Max
-0.27938 -0.05345 -0.00346  0.04975  0.54808

Coefficients:
                                 Estimate Std. Error t value Pr(>|t|)
(Intercept)                      1.846e+00  4.513e-01    4.091  4.3e-05 ***
year                            -7.069e-04  2.267e-04   -3.118 0.001821 **
factor(lon.lat.cat)east south   -3.354e+00  1.010e+00   -3.322 0.000895 ***
factor(lon.lat.cat)west north    1.116e+00  5.932e-01    1.881 0.059973 .
factor(lon.lat.cat)west south    6.983e-01  8.524e-01    0.819 0.412690
factor(kjonn)2                   1.017e+00  5.136e-01    1.981 0.047585 *
alder                           -2.219e-02  1.896e-01   -0.117 0.906827
year:factor(lon.lat.cat)
east south                       1.642e-03  5.071e-04    3.238 0.001203 **
year:factor(lon.lat.cat)west north-5.579e-04  2.981e-04   -1.872 0.061246 .
year:factor(lon.lat.cat)west south -3.782e-04  4.283e-04   -0.883 0.377259
year:factor(kjonn)2             -5.191e-04  2.580e-04   -2.012 0.044254 *
year:alder                       1.225e-05  9.526e-05    0.129 0.897696
factor(lon.lat.cat)east
south:factor(kjonn)2             6.202e-03  1.983e-03    3.128 0.001760 **
factor(lon.lat.cat)west
north:factor(kjonn)2             6.113e-04  1.206e-03    0.507 0.612100
factor(lon.lat.cat)west
south:factor(kjonn)2             3.691e-03  1.708e-03    2.161 0.030724 *
factor(lon.lat.cat)east
south:alder                      1.087e+00  4.452e-01    2.440 0.014670 *
factor(lon.lat.cat)west north:
alder                           -4.310e-01  2.499e-01   -1.725 0.084609 .
factor(lon.lat.cat)west
south:alder                     -6.108e-01  3.628e-01   -1.683 0.092293 .
factor(kjonn)2:alder            -5.475e-01  2.170e-01   -2.523 0.011621 *
year:factor(lon.lat.cat)
east south:alder                -5.311e-04  2.236e-04   -2.375 0.017551 *
year:factor(lon.lat.cat)
west north:alder                 2.136e-04  1.256e-04    1.701 0.088997 .
year:factor(lon.lat.cat)
west south:alder                 3.135e-04  1.824e-04    1.719 0.085645 .
year:factor(kjonn)2:alder        2.778e-04  1.090e-04    2.548 0.010850 *
```

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07914 on 90911 degrees of freedom
Multiple R-squared:  0.02057,  Adjusted R-squared:  0.02033
F-statistic: 86.77 on 22 and 90911 DF,  p-value: < 2.2e-16
```

```
For  vs1mm

Call:
lm(formula = vs1mm ~ alder + factor(kjonn) + factor(lon.lat.cat) +
    alder:factor(kjonn) + factor(kjonn):factor(lon.lat.cat) +
    alder:factor(lon.lat.cat) + Temperature + SumB + sumsize,
    data = s15)

Residuals:
     Min       1Q    Median       3Q      Max
-0.20000 -0.04334 -0.00072  0.04294  0.40929

Coefficients:
                                                Estimate Std. Error t value Pr(>|t|)
(Intercept)                                    2.136e-01  2.356e-03  90.669  < 2e-16 ***
alder                                         -1.971e-02  7.875e-04 -25.021  < 2e-16 ***
factor(kjonn)2                                -1.627e-03  1.381e-03  -1.179 0.238514
factor(lon.lat.cat)east south                  5.416e-03  2.116e-03   2.559 0.010490 *
factor(lon.lat.cat)west north                 -1.900e-02  2.901e-03  -6.548 5.86e-11 ***
factor(lon.lat.cat)west south                 -6.297e-02  2.357e-03 -26.714  < 2e-16 ***
Temperature                                    2.212e-02  3.195e-04  69.217  < 2e-16 ***
SumB                                           3.776e-04  1.069e-04   3.531 0.000413 ***
sumsize                                       -3.171e-03  8.956e-05 -35.406  < 2e-16 ***
alder:factor(kjonn)2                           4.655e-03  5.184e-04   8.979  < 2e-16 ***
factor(kjonn)2:factor(lon.lat.cat)east south -6.187e-03  9.969e-04  -6.207 5.43e-10 ***
factor(kjonn)2:factor(lon.lat.cat)west north -5.286e-03  1.155e-03  -4.576 4.74e-06 ***
factor(kjonn)2:factor(lon.lat.cat)west south -5.818e-03  1.136e-03  -5.121 3.04e-07 ***
alder:factor(lon.lat.cat)east south            7.861e-03  8.148e-04   9.647  < 2e-16 ***
alder:factor(lon.lat.cat)west north            6.113e-03  1.222e-03   5.003 5.64e-07 ***
alder:factor(lon.lat.cat)west south            2.687e-02  8.845e-04  30.377  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.06293 on 127719 degrees of freedom
Multiple R-squared:  0.07581,  Adjusted R-squared:  0.0757
F-statistic: 698.4 on 15 and 127719 DF,  p-value: < 2.2e-16


>



For vs1mm/vs2mm

> summary(M3)
```

```
Call:
lm(formula = df ~ alder + factor(kjonn) + factor(lon.lat.cat) +
    alder:factor(lon.lat.cat) + alder:factor(kjonn):factor(lon.lat.cat) +
    Temperature + SumB + sumsize, data = s16)

Residuals:
     Min       1Q   Median       3Q      Max
-0.35725 -0.05071 -0.00108  0.04907  0.56288

Coefficients:
                                          Estimate  Std. Error t value Pr(>|t|)
(Intercept)                               3.184e-01  2.872e-03 110.874   <2e-16 ***
alder                                    -5.540e-04  1.002e-03  -0.553   0.5805
factor(kjonn)2                           -4.010e-03  1.835e-03  -2.185   0.0289 *
factor(lon.lat.cat)east south            -3.421e-02  2.482e-03 -13.783   <2e-16 ***
factor(lon.lat.cat)west north            -5.078e-03  3.413e-03  -1.488   0.1369
factor(lon.lat.cat)west south            -7.661e-02  2.766e-03 -27.700   <2e-16 ***
Temperature                               3.030e-02  3.848e-04  78.744   <2e-16 ***
SumB                                      5.189e-03  1.288e-04  40.300   <2e-16 ***
sumsize                                  -3.533e-03  1.078e-04 -32.764   <2e-16 ***
alder:factor(lon.lat.cat)east south       1.186e-02  1.018e-03  11.650   <2e-16 ***
alder:factor(lon.lat.cat)west north       1.878e-05  1.502e-03   0.013   0.9900
alder:factor(lon.lat.cat)west south       2.574e-02  1.106e-03  23.270   <2e-16 ***
alder:factor(kjonn)2:factor
(lon.lat.cat)east north                   9.940e-04  8.507e-04   1.168   0.2426
alder:factor(kjonn)2:factor
(lon.lat.cat)east south                  -1.981e-04  5.900e-04  -0.336   0.7371
alder:factor(kjonn)2:factor
(lon.lat.cat)west north                   6.713e-04  9.112e-04   0.737   0.4613
alder:factor(kjonn)2:factor
(lon.lat.cat)west south                   7.062e-04  6.519e-04   1.083   0.2787
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.07577 on 127719 degrees of freedom
Multiple R-squared:  0.1019,   Adjusted R-squared:  0.1018
F-statistic: 966.3 on 15 and 127719 DF,  p-value: < 2.2e-16
```