MASTER OF SCIENCE IN MARINE BIOLOGY - FISH BIOLOGY

Metapopulation dynamics in Atlantic herring (*Clupea harengus* L.) along the coast of southern Norway and in the local area of Landvikvannet

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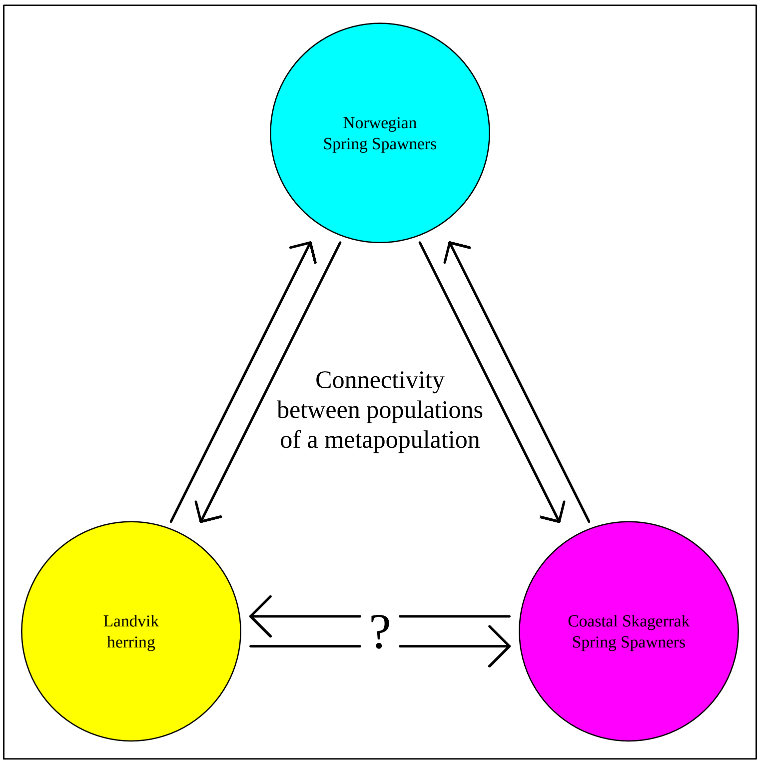

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ABSTRACT

The present thesis provides strong indications for metapopulation dynamics occurring in Atlantic herring (*Clupea harengus*) along the Norwegian south coast. The evidence stems from analyses of population structure, growth, maturation, spawning time and migration at three different scales. Firstly, comparisons between three oceanic areas (southern and northern North Sea and Skagerrak/Kattegat), two coastal areas (east and west coast of southern Norway) and one local area (Landvikvannet and connected fjords) using historic data from 1970–2012. Secondly, a detailed study of the biological dynamics in the local area over the spawning season 2012. Thirdly, a study of individual migration behavior of tagged herring using acoustic transmitters in the local area over the spawning season 2012. The historical data demonstrated intra- and inter-annual stability in population structure and growth in the southern and northern North Sea. However, in Skagerrak/Kattegat as well as in the coastal and local areas it was highly dynamic. Moreover, the data on maturation and spawning time demonstrated very little overlap between the oceanic areas and the coastal ones, whereas spawning time overlapped clearly between herring diverging phenotypically from the west coast, east coast and in the local area, indicating that mixing of populations during spawning activities potentially could have happened. When this was studied in more details with the intensive biological sampling regime in the local area of Landvik and connected fjords during the spring 2012, data on otolith characteristics, vertebral counts and growth indicated the mixed presence of three different herring types during the spawning period. Herring caught inside Landvikvannet (ILV) had significant lower mean vertebral counts (VS) and lower growth than herring caught outside Landvikvannet in the connected fjords (OLV). Migratory Norwegian spring spawners (NSS) arrived early in the season with peak abundance in mid-March, and they could be identified through otolith characteristics, higher growth and VS (above 57.0) than the other two groups in the local area. While the growth and VS of NSS did not differ significantly within the spawning season, they decreased for ILV and OLV herring, suggesting a mixture of two components changing with time in both areas. The data indicated that one component with relatively fast growth and medium VS between 56.5 and 56.9 appeared early in the season already at the onset of sampling in February and stayed there the whole period. In addition, there was a slow growing component with low VS (below 56.0), similar to historic observations of ILV herring in May, which did not appear early in the season, peaking in May. Despite the different peaks of abundance between the three suggested components, there was a clear overlap in spawning stages. Acoustic telemetry of tagged herring also demonstrated behavioral differences within the local area, which support the conclusion of mixing herring populations in the area. While some herring left the study area immediately, others stayed for a while, migrated up and down in the connected fjords or even entered Landvikvannet. Most migrations took place during the evening and night. Additionally some herring were detected in another acoustic monitoring system 20 km to the north of the study system 2 to 35 days after leaving the area, demonstrating along-coast migrations at different speeds. Finally, relevant historical environmental data series and new environmental data collected during the 2012 spawning season in Landvik and connected fjords were analyzed in relation to the observed herring dynamics at the three different scales. They did not show any significant influence on the intra- and inter-annual variations of biological parameters like growth, VS and maturation, supporting that the observed dynamics rather indicate a mixture of populations changing both historically and over the year. However, the high temperature and low salinity observed in the historic time series from Landvikvannet in May could clearly explain the very low VS observed. Moreover, the observed decrease in VS over the 2012 spawning season in Landvik and connected fjords was significantly related to increasing temperatures, which could indicate a tendency of herring returning to spawn in the same part of the season and in similar environment as their parents. To conclude the combination of data at different scales clearly suggests high dynamics in population structure along the south coast of Norway, and even though differentiation in peak spawning may occur the clear overlap in spawning stages observed in herring diverging phenotypically provides strong indications of regular interbreeding between populations, thereby supporting the metapopulation concept.

Keywords: *Clupea harengus*, metapopulation, population structure, Atlantic herring, vertebrae, acoustic telemetry.

1 INTRODUCTION

The basis for studying population structure in fish is the objective to manage and exploit a fish species sustainably, securing maximum sustainable yield and at the same time avoiding collapses through limitations in fishery in periods of low recruitment and biomass(Sinclair and Solemdal, 1988; Smedbol and Stephenson, 2001; Stephenson, 2001). Typically, fish species may be split into populations based on their degree of reproductive isolation from each other in space and/or time, which could be reflected in genetic or phenotypic differences driven by diverging environmental conditions (Heincke, 1898; McPherson et al., 2001; Sinclair and Iles, 1988). Under such circumstances exploitation of one population should have little effect on the population dynamics of a neighboring population, and therefore it is also common to assess and manage such populations separately (Cochrane, 2002; Wallace and Fletcher, 1997). On the other hand, there are also examples where populations are recognized to be separate with diverging spawning season and/or spawning area, but due to mingling in other seasons separate management of the populations may be difficult (Ruzzante et al., 2006; Stephenson et al., 2009). Fisheries biologists therefore often use the term stock instead of population in their fisheries advice; i.e. sometimes a species is harvested and therefore managed as one stock and at other times as several separate stocks. In Begg et al. (1999) the concept of a fish stock was simply defined as characteristics of semi-discrete groups of fish with some definable attributes, which are of interest to fishery managers. However, Begg et al. (1999) summarized the results from a symposium on stock identification, where the need to identify fish stocks more accurately and the implications for fisheries management were clearly emphasized. Hence, the understatement is that in many cases lack of knowledge may lead to the convenience of harvesting populations as one stock. Improved knowledge of population structure and splitting into more stocks could therefore lead to more sustainable management, securing a higher diversity within the species.

The population structure of Atlantic herring (*Clupea harengus* L.) is known to be highly complex (Iles and Sinclair, 1982). Herring is an iteroparous clupeid maturing first time at two or three years of age and a total spawner that aggregate at high densities and deposit their sticky eggs on shells, gravel, coarse sand and small stones at depths down to 250 m (Runnstrøm, 1941a). The larvae hatch after 2–4 weeks depending on temperature (Meyer, 1878; Soleim, 1942), and the larvae drift with the currents until metamorphosis (Corten, 1986; Dragesund et al., 1980; Russell, 1976), yet with some vertical migration (Blaxter and Parrish, 1965; Woodhead and Woodhead, 1955). The population separation is based largely on differences in spawning locations through major geographical barriers with little mixing of larvae, phenotypic differences like spawning time, otolith characteristics and meristic characters (Bekkevold et al., 2007; Clausen et al., 2007; Heincke, 1898; Hulme, 1995) as well as genetic structure (Andre et al., 2011; Bekkevold et al., 2005; Jørgensen et al., 2005; Limborg et al., 2012). The actual dynamics of population structure of Atlantic herring have been widely discussed, e.g. the discrete population concept (member/vagrant hypothesis) (Sinclair and Iles, 1989) and the metapopulation concept (adopted migrant hypothesis) (McQuinn, 1997). A metapopulation is composed of two or more distinguished subpopulations with variable but moderate interbreeding and significant gene flow, whereas discrete populations are reproductively isolated through closed life cycles and a limited gene flow (McQuinn, 1997). The occurrence of temporal and spatial overlap during spawning allows genetic exchange between subpopulations, which is a prerequisite for the existence of metapopulations.

One may questions whether the metapopulation concept could be used to explain the variety of herring described in Norwegian waters. Some herring found along the Norwegian coast and inside the fjords are suggested to be rather stationary with adaptations to local conditions, being phenotypically and in some occasion genotypically different from the nearby oceanic population. Some examples of such local populations are the Trondheimsfjord herring (Broch, 1908; Runnstrøm, 1941b), Borge Poll herring (Rasmussen, 1942), the Lusterfjord herring (Aasen, 1952), the Lindåspollene herring (Lie et al., 1978), the Balsfjord herring (Jørstad and Pedersen, 1986), the Lake Rossfjord herring (Hognestad, 1994) and the summer/autumn spawners in northern Norway (Husebø et al., 2005). Despite these findings, the overall research effort targeting local populations along the Norwegian coast has been rather low, and it is therefore expected that there may be several more local populations. Johannessen et al. (2009) obtained evidence for the metapopulation concept at the Norwegian west coast where herring from two different populations appeared to mix during the spawning season in Lindåspollene, and it is likely that similar mixing also may occur in other locations along the coast. An important mixing area for herring is the eastern North Sea and Skagerrak, where at least three different stocks, North Sea Autumn Spawners (NSAS), Western Baltic Spring Spawners (WBSS) and Norwegian Spring Spawners (NSS) occur during the year. They can be distinguished by spawning site, timing of spawning season and meristic characters such as the number of vertebrae and otolith characteristics (Clausen et al., 2007; Johannessen et al., 2009).

Mixing among herring stocks in the eastern North Sea and Skagerrak is related to their life history and annual migrations. Pelagic herring larvae of NSAS hatched in autumn and winter along the British North Sea coast drift several hundred kilometers across the North Sea over a few months ending in the Skagerrak, Kattegat and inner Danish waters during January until March (Johannessen and Moksness, 1991). The larvae and juveniles of NASA may feed in this area for some years before returning to their spawning locations in the western North Sea (Iles and Sinclair, 1982). After spawning from March to May in the area off the island Rügen WBSS migrate to feeding areas in Kattegat, Skagerrak and eastern North Sea, also juvenile WBSS, generally at the age of 2, may drift out of the Baltic and enter this area during the summer (Biester, 1979). In contrast to NSAS and WBSS the Norwegian spring spawning herring may use the North Sea area down to Skagerrak as spawning grounds. In mid-January NSS commence their spawning migration from northern Norway after having spent the wintering period there. The adult individuals reach the spawning grounds from Lofoten (69° N) in the north to Lista (57.5° N) in the south of Norway during February until March (Dragesund et al., 1997; Røttingen and Slotte, 2001; Slotte, 1999b). NSS have also been observed to mix with

NSAS during the summer and autumn in northeastern North Sea (Dragesund and Haraldsvik, 1968; Haraldsvik, 1968). However, no clear evidence for migration of NSS to the east of Lista and into the Skagerrak area has been published. Devold (1963) hypothesized that the shifts in periods with large concentrations of herring in the Bohuslän area was due to NSS, shifting their spawning grounds back and forth between the Norwegian west coast and the Bohuslän coast. However, this was later disproved by Höglund (1972) demonstrating that this was NSAS, and not NSS herring. Corten (1999) followed up on this and proposed that the mechanism behind the Bohuslän periods was simply shifts in NSAS wintering area occurring in periods with large new year classes coming in and persistent easterly winds.

In addition to NSS, NSAS and WBSS, there are probably local spring spawners at several locations around Skagerrak. With the exception of Rosenberg and Palmén (1982) and Bekkevold et al. (2005), studies published on the population structure, biology and behavior of these Skagerrak spring spawners are lacking in the literature, and they are not treated at all in the assessment and management of herring in the area (ICES, 2012). However, the Institute of Marine Research (IMR) in Flødevigen has over many years sampled adult spring spawning herring along the coast of southern Norway during annual research surveys, by sampling the commercial fishery in the coastal and fjord areas and by own gill netting. Some of this is sparsely reported in internal documents, but nothing has been properly published in the international peer review literature based on the analyses of all these herring. One of the more interesting locations with spring spawners is the brackish locality inside Landvikvannet, an inland lake artificially connected to the open sea through a canal, which has been regularly sampled for herring since the 1980s. The herring caught in the lake normally are very ripe or with running gonads and they have low mean vertebral number, below 56. In addition, Silva et al. (2013) showed that this particluar herring has high fecundity and low growth rate. This has led to the hypothesis that the lake on annual basis is visited by a herring population with special adaptations to spawning in the brackish environment, even though actual spawning, eggs or larvae never have been observed. In addition, in the coastal areas outside the lake, both to the east and west, samples of spring spawning herring with mean vertebral numbers above 56 and even above 57 has occurred, indicating that there may be a mixture of several populations in the area. The present study is based on the conviction that this historic and unpublished material from an area with potential high dynamics and mixing could be of great value for increasing the knowledge of population structure in herring, testing the metapopulation concept and ultimately modify the herring management in the area.

To understand the interactions and relationship between the herring populations mixing in the Landvik area and along the coastline it is also essential to learn more about the herring behavior at the individual and the collective school levels. Tracking the movements of fish with acoustic receivers has become an adequate tool during the last years (Hightower et al., 2001; Pine et al., 2003). In the beginning the tagged individuals had to be followed manually but due to new techniques it is now possible to set out receiver units covering a certain area and saving the signals of the transmitters automatically. This method was used successfully for individuals of various species like blacktip shark (*Carcharhinus limbatus*) (Heupel and Simpfendorfer, 2002), cod (*Gadus morhua*) (Olsen and Moland, 2011) or pigeye shark (*Carcharhinus amboinensis*) (Knip et al., 2011). Compared to herring the three example species are much larger and not so highly sensitive to handling and scale loss and therefore much easier to tag. However, Langård et al. (2012) have used this technique for the first time on herring and evaluated this new acoustic tagging methodology as suitable for behavioral investigations.

Based on the information above the main objective of the present study was to explore if the metapopulation concept could describe the dynamics in herring population structure appearing at the Norwegian south coast by analyses at three different scales. Scale 1: to conduct thorough statistical analyses of the available time series of biological data collected and analyzed by IMR in the North Sea, Skagerrak and Kattegat area, including the Norwegian coastline and especially the Landvik location, in order to study the potential overlap in time, space and maturity between herring diverging phenotypically. Scale 2: to carry out biological sampling and analyses of data collected over an entire spawning season in the Landvikvannet and connected fjord area, to study potential temporal changes in population structure and mixing of herring diverging phenotypically during spawning. Scale 3: to carry out tagging experiments on pre-spawning herring in Landvikvannet and connected fjords using acoustic monitoring methodology to track the individual behavior, in order to study potential diverging migration behavior during and after spawning. And additional objective was to analyze historical time series of environmental data collected by the IMR in the studied areas, as well as detailed environmental data sampled over one spawning season in Landvikvannet and connected fjords in conjunction with biological sampling and tagging, to explore if the results gained from the herring analyses at the three different scales could be related to changes in environmental conditions.

2 MATERIAL AND MEHTODS

2.1 Biological samples: oceanic, coastal and local

In order to study potential metapopulation dynamics at the coast of southern Norway, biological samples collected in the oceanic areas of the North Sea, Skagerrak and Kattegat were compared with those observed along the coast and in the local area of Landvik. The split into areas and the data sets used are described in the following.

As part of analyses of historical biological data at scale 1, data were included from the IMR database from both oceanic and coastal areas from 1970–2012. Oceanic data including commercial and scientific catches in the North Sea, Skagerrak and Kattegat were split into 3 different data sets (Table 1 and Table 2). Oceanic data are defined as samples collected outside the territorial waters, 12 nm off the coast, of Norway. The data were pooled into a northern North Sea (NNS) (area 42, 28 and 08), a southern North Sea (SNS) (area 41) and a Skagerrak and Kattegat (SK) data set (area 09) (Figure 1). Different fishing methods like bottom, pelagic or prawn trawls, seine fishing, gillnet or line and hooks were used to sample herring in oceanic areas (Table 3). Both North Sea areas include spawning grounds of the NSAS. On one hand the Shetland Islands and Buchan at the northeastern Scottish coast are located in the northern area, on the other hand the Dogger Bank and Downs, whereas the latter one is located outside of the sampling area, in the southern region. The third oceanic area, Skagerrak and Kattegat, is an important feeding, mixing and nursery ground of Atlantic herring populations.

Coastal data were sampled within the territorial waters of Norway from 1970–2012 to the west of Lindesnes (7° W) up to 62° N along the coast (WC) in locations of the areas 08 and 28, and to the east of Lindesnes in locations along the Skagerrak coast of Norway (EC) in area 09 (Table 1 and Table 2). In addition to the used sampling methods for the oceanic data purse seine and bottom/floating nets were used to collect coastal data (Table 3). Between 1980 and 2011 different samples were collected, including spring spawning herring only, along the Skagerrak coast in area 09. Included in the coastal data of spring spawners in the Skagerrak two samples were collected along the coast of Sweden (see Figure 1). The spring spawning herring along the eastern coastline of Norway were caught by pelagic trawls, seine fishing (without purse seine), and gill, bottom and floating nets. Coastal data were pooled into 2 different data sets, a western and eastern set. The eastern coast is known as spawning ground of the spring spawning herring (Rosenberg and Palmén, 1982), but not for the Norwegian spring spawners (Røttingen and Slotte, 2001). NSS spawning grounds can be found along the coast of western Norway Dragesund et al. (1997).

Table 1: Total number of analyzed herring per month for oceanic, coastal and local (Landvikvannet and connected fjords) area from 1970-2012. Local data from 2012 were excluded and included in Table 4. One year old and younger herring were excluded.

Month	NNS	SNS	SK	WC	EC	LV
1	4479	1387	424	222	469	
2	3774	1397	7	3738	2625	
3	3052	266	175	11936	4512	
4	2032	29		3733	3338	100
5	13921	1720	1235	2483	749	1388
6	30717	2780	1894	981	446	122
7	34194	3424	1590	2032	388	
8	3616	1461	817	749	364	
9	2341	418	40	388	607	
10	3750	384	162	291	1453	
11	5697	1095	177	1427	5666	
12	1709	176	354	211	757	
Total	**109282**	**14537**	**6875**	**28191**	**21374**	**1610**

Table 2: Total number of analyzed herring per year for oceanic, coastal and local (Landvikvannet and connected fjords) area from 1970–2012. Local data from 2012 were excluded and included in Table 4. One year old and younger herring were excluded.

Year	NNS	SNS	SK	WC	EC	LV
1970	1678	817	428	63		
1971	990	15	172			
1972	865	503	115	99	78	
1973	1522	222	98		90	
1974	1817	674		21		
1975	1971	17		94		
1976	1579	298		1	194	
1977	900		5	154	20	
1978			272	134	169	
1979	143	31	222	598		
1980	486	5	358	668	1789	
1981	633	477	192	505	1014	
1982	913		88	583	1126	
1983	1530	333	92	1102	2322	
1984	3188	284		656	1979	134
1985	4045	293	411	690	1237	97
1986	2284	676	17		586	
1987	4056	635	45		607	
1988	3601	1300	277	507	777	
1989	4794	293	162	1195	380	
1990	4833	240	378	1080	549	
1991	4618	809	58	1046	592	100
1992	3540	466	337	3677	864	
1993	3178	893	246	1809	187	100
1994	4426	47	1	185	356	56
1995	5052	718	233	674	620	99
1996	2713	526	188	781	322	95
1997	4390	566	334	1739	400	96
1998	4355	131	325	2693	307	98
1999	3589	319	595	1969	455	50
2000	3564	59	476	1681	327	99
2001	3582	732	650	471	352	99
2002	4362	214		152	643	
2003	3608	467		406	926	
2004	2411	94	100	101	275	
2005	3336	315		275	329	
2006	2073	270		28	281	
2007	1252	50		123	68	
2008	931	38		165	164	
2009	578	253		450	95	50
2010	1028	211		666	442	244
2011	2452	87		692	452	193
2012	2416	159		258		
Total	**109282**	**14537**	**6875**	**28191**	**21374**	**1610**

Table 3: Total number of analyzed herring with different sampling methods for oceanic, coastal and local (Landvikvannet) area from 1970–2012. Local data from 2012 were excluded and included in Table 4. One year old and younger herring were excluded.

Method	NNS	SNS	SK	WC	EC	LV
Bottom trawl	7086	2384	444	217		
Pelagic trawl	28414	2501	1238	4226	4340	
Prawn trawl	3953	872	246	2164	261	
Seine fishing	68466	8750	4711	17912	5610	
Purse seine				98	177	
Gillnet	533			2952	4794	1610
Bottom/Floating nets				451	6158	
Line and hook			67	63		
Unspecific	830	30	169	108	34	
Total	**109282**	**14537**	**6875**	**28191**	**21374**	**1610**

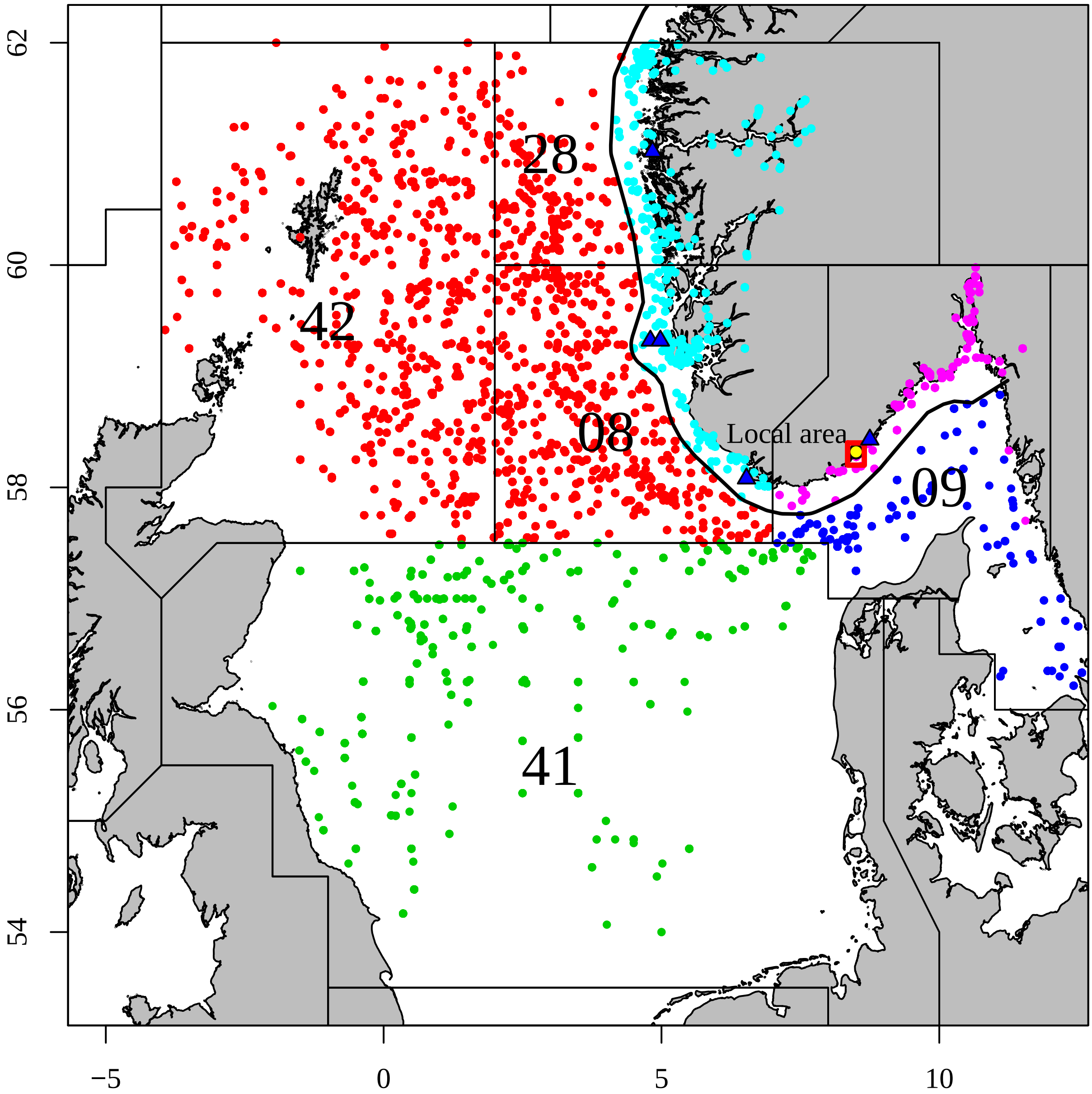

Figure 1: Statistical areas of the North Sea, including sampling stations from 1970–2012 of biological data in the northern North Sea (red), southern North Sea (green), Skagerrak and Kattegat (blue), west coast (cyan), east coast (purple) and Landvikvannet (yellow) and environmental data (blue triangles), thick black line = 12 nm zone, one year old and younger herring were excluded.

Since 1984 local data of Lake Landvik (Landvikvannet = LV) was collected during April–June (mostly in May) on an annual basis, while data from the connected fjords were sampled from 1980–2011 (Table 1 and Table 2). The data of the connected fjords were pooled together with the data set of the east coast. Landvikvannet was pooled as a single data set.

As part of analyses of biological data and potential metapopulation dynamics at scale 2, samples were collected from Landvikvannet and connected fjords over a full spawning season in 2012, starting in February and ending in August (Table 4). The collected data were separated into two data sets; data from inside of Landvikvannet (ILV) and data from the connected fjords outside of Landvikvannet (OLV). All local data were exclusively captured by gillnets. In 2012 the focus for the biological data was in Landvikvannet as well as the inner part of Strandfjorden, one of the connected fjords (Figure 2). In addition two samples were conducted in Bufjorden and two in the outer part of Strandfjorden. Floating gillnets were used with a mesh size of 26 mm and 29 mm. The used gillnets had a depth of 8 m and a length of approximately 10 m. Gillnets were used for 24 hours.

Table 4: Total number of caught herring in the local area for 2012 (ice = no sampling possible because the area was covered by ice).

Date	Landvikvannet	Inner Strandfjorden	Outer Strandfjorden	Bufjorden
15/2	ice	ice	28	11
6/3	4	129	119	
20/3	47	542		
26/3	115	486		100
11/4	290	663		
14/5	177	69		
21/6	82	66		
22/8	10	0		
Total	**725**	**1955**	**147**	**111**

Given the detailed sampling and large emphasis put on the local area studied, some further descriptions of the special characteristics are given. Landvikvannet (Figure 2), southwest of Grimstad, is a ca. 1.85 km² brackish lake. In 1877 it was artificially connected to the open sea through a ca. 3 km long canal, called Reddal canal. This narrow canal, 1–4 m deep, causes the brackish environment in Landvikvannet. Since the canal opened in 1877 the water level has decreased by 3 m. At the beginning of the lake is a small 25 m deep basin. After that the depth decreases very fast up to 7–10 m all over the lake. Due to the tides there is inflow of saltwater into the lake, while freshwater empties into the lake from rivers resulting in different layers of water. The heavy saltwater stays near the bottom covered by freshwater in the upper layer. Without any exchange or circulation of the saltwater the oxygen is depleted in the lower layer. However, the circumstances cause a layered water system with anoxic bottom and an oxygen rich surface layer. In Landvikvannet herring were caught together with trout (*Salmo trutta*) and other freshwater fish by floating gillnets after the canal was opened, demonstrating that a new species had adapted to the lake. Most of the shoreline is covered by reed; otherwise the shore is rocky and very steep.

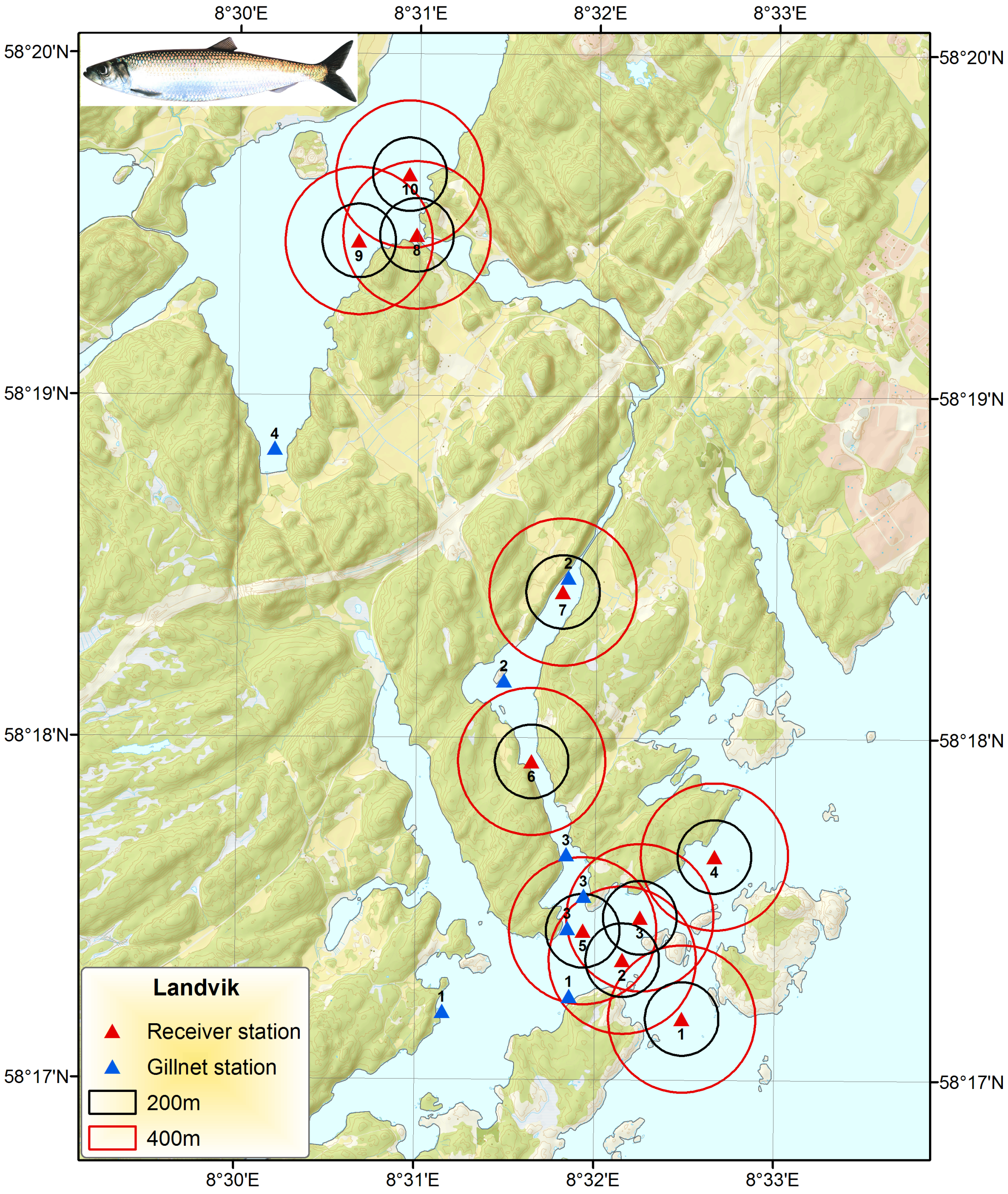

Figure 2: Map of the study area, red stations show the deployed receiver stations with the minimum radius of 200 m (black) and the maximum radius of 400 m (red), blue stations show the different sampling stations for the gillnet survey (1 = Bufjorden, 2 = Inner part of Strandfjorden, 3 = Outer part of Strandfjorden, 4 = Landvikvannet).

The abiotic factors of Strandfjorden are typically for an open sea environment. Catches included herring, cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) mainly and were caught by floating gillnets. The fjord was divided in two parts, the inner and outer Strandfjorden. In total, the fjord is approximately 2 km long. The outer Strandfjorden is the narrow part, 1–7 m deep, and the inner part is deeper, 10–13 m. Most samples were collected in the inner part, close to Reddal canal. The shore is rocky and very steep with some seaweed in the first meters. Deeper than 5–6 m the bottom becomes sandy and muddy.

The last fjord in the study area is Bufjorden which is a small fjord having direct access to the Skagerrak. At the beginning of Bufjorden is a 54 m deep basin. The abiotic factors are similar to those in Strandfjorden. Bufjorden can be entered from two different directions, from the south or east. The southern exit is round about 30 m deep, while the eastern exit is 14 m deep. From the basin in Bufjorden, Strandfjorden can be reached at a depth of approximately 15 m. During the study period only two biological samples were taken in Bufjorden. Due to the open access to Skagerrak this is an important area for the telemetry experiments where 5 of 10 telemetry receivers are moored, see chapter 2.3 (Telemetry data and tagging).

2.2 Biological data

The oceanic, coastal and local herring samples included in the present study were all analyzed according to the IMR standard (Mjanger et al., 2010). Data were collected throughout the study period in the described study areas at scales 1–2 (Table 1–4, Figure 1–2) to identify the herring population and its biological status with regard to maturation. Normally the sample size comprised 100 herring, but this number could be reduced and limited to the actual catch. Biological parameters analyzed included total length (nearest 0.5 cm below), weight (nearest gram below), sex, stage of maturity, age reading from otoliths and gonad weight. Also the number of vertebrae was counted to calculate the mean vertebral counts (VS). The maturity stages have been determined by visual inspections of gonads according to the following scale: immature = 1–2, maturing = 3–4, ripe = 5, spawning/running = 6, spent = 7 and recovering = 8 (Mjanger et al., 2010). In order to study potential population dynamics immature herring (1 year old or younger) were excluded for the analyses due to a lack of knowledge to which population they belong to, e.g. they could use the area as a nursery ground only (Holst and Slotte, 1998). Additionally the gonadosomatic index (GSI) and the gonad condition (gonadK) were estimated to describe the development of gonads and the investment in reproduction as:

$$GSI = \frac{100 \times gonad\,weight}{somatic\,weight}\% \tag{1}$$

$$gonadK = \frac{100 \times gonad\,weight}{total\,length^3}\% \tag{2}$$

In the detailed study in Landvik and connected fjords in 2012, other fish than herring were counted, lengths were measured and the stomachs were investigated for herring eggs/larvae.

During the different scientific surveys herring were designated as Norwegian spring spawners, North Sea autumn spawners or local herring, due to the place/time of capture or due to the aim of the survey. However, this separation has no relevant effect on the data, e.g. the mean vertebral count or growth were the same for marked NSS and NSAS when they were collected at the same place and time, but just due to the aim of the survey marked as different populations. Only in 2012 a clear separation could be done based on otolith differences. Herring caught in Landvikvannet and herring from the connected fjords were identified as NSS and ILV herring or OLV herring, respectively. This was based on a subjective evaluation of the otolith by an experienced reader. The main reason for splitting was that otoliths of NSS herring (Figure 3) have much clearer distinction between winter and summer rings than local spring spawners (Figure 4), and the shape of the otoliths is more rounded for NSS.

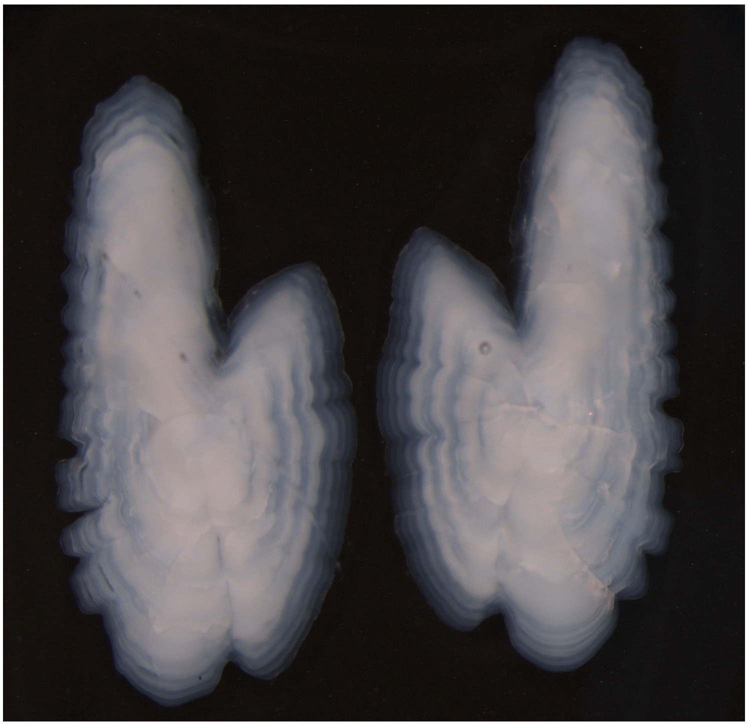

Figure 3: Otoliths of NSS, clear separation between winter and summer rings, more rounded.

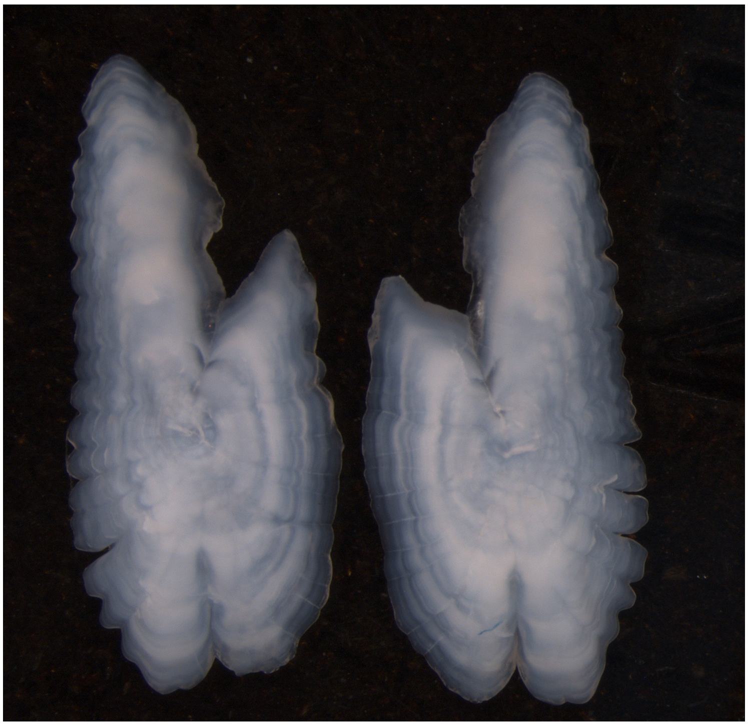

Figure 4: Otoliths of coastal spring spawners, with diffuse winter and summer rings.

2.3 Telemetry data and tagging

In the beginning of March 2012 ten acoustic monitoring receiver units (Figure 5) were moored at different geographical locations inside the study area (Figure 2). The locations were chosen according to cover all migrating activities from Landvikvannet into Skagerrak. The receiver units consist of one ultrasonic receiver (VR2W-69kHz Acoustic Monitoring Receiver, Vemco Division, Amirix Systems Inc., Halifax, Canada), one trawl float, two ropes and two weights. The ultrasonic receivers have an estimated detection radius of 200–400 m and an estimated operating time of at least 15 months. The mooring for these units consists of a 40 kg weight, followed by 6 m rope. This rope is necessary to lift the receiver for downloading the data several times during the study period. The next part is a 9 kg weight, called ”dead man”, from which a rope goes vertical upwards. The length of the rope depends on the depth of the ”dead man”. It ends with the trawl float approximately 2.5 m below the surface. The receivers were deployed by cable ties to the rope at 3 m depth with the listening station pointed downwards, except for the three units in Landvikvannet. There the listening station pointed upwards, because no fish is expected below 4–6 m due to the lack of oxygen/or low oxygen content.

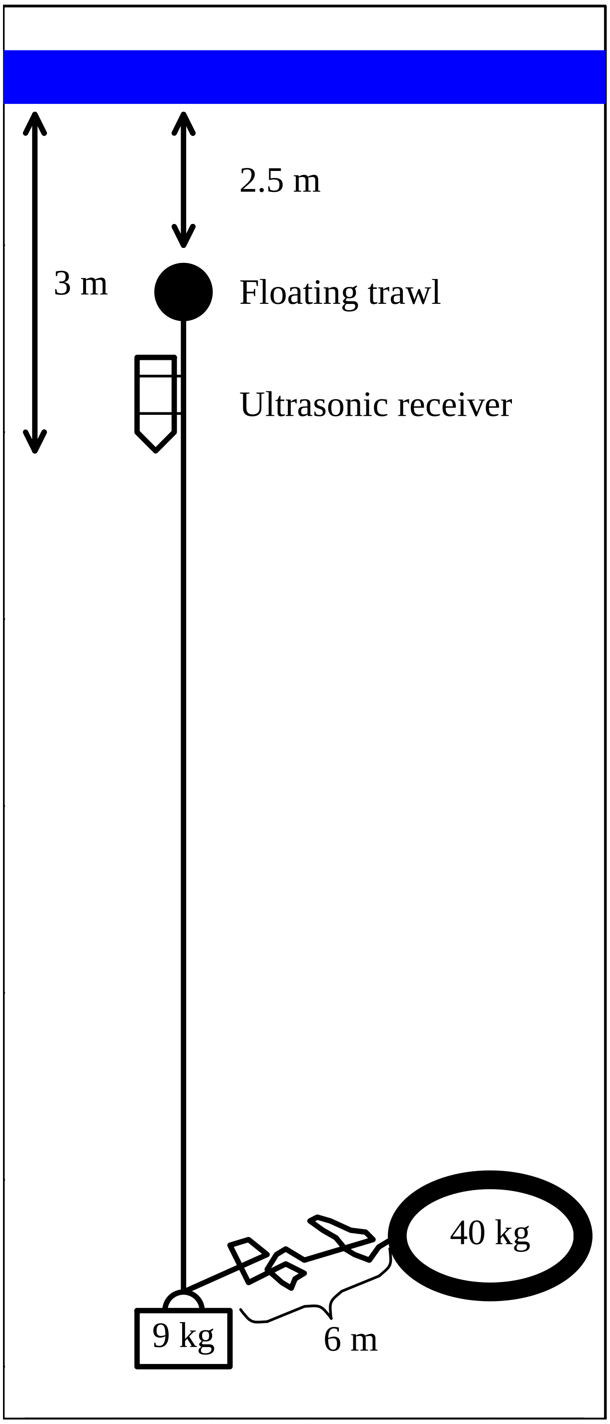

Figure 5: Schematic illustration of the receiver unit moored in the study area.

Three receiver units were moored in Landvikvannet, the first one (8 Landvikvannet E) intended to recognize all fish entering the lake. The other two were located west (9 Landvikvannet W) and north (10 Landvikvannet N) of the first receiver unit to get an overview in which direction, the tagged herring swim. For detecting the swimming direction the range of these three receivers were overlapping. In the end of Strandfjorden close to Reddal canal the next unit (7 Mollands–kjær) was moored covering the entrance to the canal. The fifth unit (6 Strandfjorden S) was placed between the inner and outer part of Strandfjorden while the sixth

(5 Nesvoll) was placed at the beginning of the outer part. With these three units all movements inside Strandfjorden were recognized. Overlapping with the range of the next two receivers the sixth receiver forms also an area where the swimming direction can be detected. One receiver was moored eastwards (3 Nesvoll E) and one (2 Skarveskjær) southwards, to cover the access area to the Skagerrak. The last two receivers were located further east (4 Nibbehausen) and south (1 Pølseskjær) to detect all individuals leaving the sampling area. Acoustic tagging data were downloaded from the acoustic monitoring receivers every 3 months.

For the purpose of acoustic monitoring of the herring behavior in Landvikvannet and connected fjord area, the fish were tagged with LP-7.3 mm acoustic transmitters (7.3 x 18 mm, weight in seawater 1.2 g, Thelma Biotel, Trondheim, Norway) and LP-9 mm acoustic transmitters (9 x 23 mm, weight in seawater 2.5 g, Thelma Biotel, Trondheim, Norway). In order to reduce code collision (i.e. two or more tags simultaneously transmitting to one receiver) transmitters were set to transmit a signal every 60–180 s with a random interval. The estimated battery life was at least one year and intended to cover two spawning seasons. The following described procedure of the tagging experiment was approved by the Norwegian Animal Research Authority. Herring were captured individually by jigging with line and hooks in the inner Strandfjorden. After capture herring were investigated for external injuries through the capture procedure or other external factors like gillnets. If neither external injuries nor abnormal swimming were observed, herring were kept on board in a big tank, 80 x 50 x 40 cm, for acclimatization. To guarantee high oxygen concentration 10 l of water were exchanged approximately every 10 min. To minimize the handling time 3 persons took part in the tagging process. Disinfected transmitters were surgically implanted in the abdominal cavity between the gonads. Therefore herring were removed from the tank by the first person, holding the herring carefully to avoid scale loss and covering the eyes to minimize stress factors. A small incision was made posterior to the pelvic fins through which the transmitter was inserted. To close the wound Histoacryl®, tissue adhesive, was used. Tagged herring were left to recover in a radius tank, 60 x 35 cm, for 30 min and monitored continuously. Tagged individuals were released close to the site where they had been caught if neither signs of injury nor abnormal swimming were observed. In addition the total length of tagged fish was measured and scales were removed for age determination.

A total of 61 herring were tagged in the course of 3 experiments. The first tagging experiment was conducted March 28–March 29 with a total of 43 tagged herring out of 55 caught individuals. For all individuals the LP-9 mm transmitters were used. Herring released after capture due to injuries or abnormal swimming were not included. However, the highest discard rate took place after capture (number unknown). Ten individuals were discarded during the tagging procedure because the wound could not be closed. Only 2 herring were discarded after tagging. A total of 13 out of 15 fish were tagged in the second experiment May 15–May 16. This time 7 herring were tagged with LP-9 mm transmitters and 6 with LP-7.3 mm transmitters. In the last experiment June 20–June 21 all 5 caught fish were tagged with LP-7.3 mm transmitters.

2.4 Enviromental data

In order to describe changes in the habitat of the herring inside Landvikvannet, data on the special environmental conditions observed in connection with the biological sampling since 1983 were analyzed (Table 5). In 2012 effort was put on the environmental sampling over the season both inside and outside the lake in order to relate the potential dynamics in population structure and spawning activities as well as individual behavior of tagged fish to environmental conditions. In general water samples were conducted at the site where gillnets were moored in the inner part of Strandfjorden (gillnet station 7 (Figure 2)) and at the beginning of Landvikvannet in the first basin (receiver station 8 (Figure 2)). A CTD system (STD/CTD – model SD204, SAIV A/S Environmental sensors and Systems, Bergen, Norway) measured temperature, salinity and depth, while the oxygen/hydrogensulfide concentration in the water samples was analyzed in laboratory at Flødevigen marine research station (Institute of Marine Research). Water samples in the lake were collected each meter to identify the exact depth where the oxygen is depleted, after that the standard interval of 5 meter was used. In addition to the sampled environmental data from Landvikvannet since 1983, data sampled on a daily basis next to the Flødevigen marine research station were used to show historical changes in environmental conditions over a long time period. The sampling of environmental data started in 1919 at depths of 0 m, 1 m, 19 m and 75 m. Since 1975 the temperature and salinity were collected daily at 9:00 a.m. In 2009 the data were collected electronically and continuous including also air temperature, wind direction and speed. Also data from 5 stations, Bud (N 62°56’ E 6°47’), Sognesjøen (N 61°01.4’ E 4°50.4’),

Table 5: Number of samples for environmental data and the collected types of data per year in Landvikvannet (* samples in Strandfjorden, $^\#$ samples in Bufjorden).

Year	Number	Temperature	Salinity	O_2/H_2S concentration
1983	1	x	x	x
1984	3	x	x	x
1987	1		x	x
1989	1	x	x	x
1991	1	x	x	x
1993	1	x	x	x
1994	1	x	x	x
1995	1	x	x	x
1996	1	x	x	x
1997	1	x	x	x
1998	1	x	x	x
1999	2	x	x	x
2000	2	x	x	x
2001	1	x	x	x
2009	1	x	x	x
2010	1	x	x	x
2011	3	x	x	x
2012	7	x	x	x
2012*	8	x	x	x
2012$^\#$	1	x	x	x

Ytre Utsira (N 59°19’ E 4°48), Indre Utsira (N 59°19’ E 4°59’), Lista (N 58°05’ E 6°32), along the west coast of Norway were analyzed from 1970–2012 (Figure 1). The most northern station Bud was outside of the study region, but will be included for the analyses of the environmental data. These stations were established by the directorate of fisheries in Norway in 1935–1947. Temperature and salinity were measured in depth of 1, 5, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250 and 300 m.

2.5 Data analysis

All data (biological, telemetry and environmental) were imported into the R software (version 2.15.1; The R Foundation for Statistical Computing 2012) for statistical analyses and plotting of results. Since sex could not be determined the telemetry data were analyzed for males and females combined. Parametric test (continuous response variable) like linear regression (continuous predictor variable(s)), analysis of variance = ANOVA (categorical predictor variables(s)) or analysis of covariance = ANCOVA (categorical and continuous predictor variables) and non-parametric test (categorical response variable) like Kruskal-Wallis- or H-test were used in the analyses. Kruskal-Wallis-test was also used for not normal distributed characters like age and total length. Stage of maturity was also handled as a non-parametric variable, since the duration of each maturity stage varied for herring (Iles, 1964) and the inspection was subjective. Therefore the stages of maturity did not represent a continuous variable; instead they were handled as a ranked and categorical variable. If more than 2 groups were analyzed with a parametric test, except for linear regressions, posterior multiple comparisons of pairs (Tukey’s range test, 95%) were done to show significant differences between the individual groups. The Wilcoxon-Mann-Whitney- or U-test and the two-sample T-test were used to show significant differences between two non-parametric or parametric characters, respectively. In order to test the significance of variables along contingency tables the Chi²-test and Fisher’s exact test were conducted. If those previous statistical tests demonstrated significant differences and the figures indicated a visible trend, the trend was tested for significance as well. Trends of parametric variables were tested with regressions, while trends of non-parametric variables were tested with the Spearman’s rank correlation coefficient. To use ANOVA or ANCOVA 3 assumptions a) samples are selected randomly from the population and independently from each other, b) the response variable in each group has a normal distribution and c) all groups have the same variance must be fulfilled. The independence and randomness of samples were given due to the sample design, the response variable was tested for normality by the Shapiro-Wilk- or W-test, and the last assumption of equal variance could not be fulfilled in all cases. This assumption is usually unrealistic and can be violated since the results are not severely affected if the group variances moderately differ from each other (Shahbaba, 2012). For all tests a level of significance $\alpha = 0.05$ was set. To reduce the influence of a high sample size (N) in the historical data a Power Analysis was conducted to calculate the minimum needed N for a small effect size (f = 0.1), significance level $\alpha = 0.05$, 6 groups and a power of 80%. Given this quantities the calculated minimum N was 214. For a standardized comparison the sample size was reduced 250 observations, producing a power of 86%. This standardization was conducted to compare the distribution of total length, age and VS for pooled data from 1970–2012 along the 6 areas. In addition, length-at-age data, followed defined as the growth of individual herring, were fitted to the von Bertalanffy growth model = VBGM (Bertalanffy, 1934). The typical VBGM is represented by

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{3}$$

where

- L_t is the average maximum length at age t,
- L_∞ is the asymptotic average length,
- K is the so-called von Bertalanffy growth rate coefficient or more precisely the rate at which length approaches the maximum length asymptote and
- t_0 represent the age when the average length was zero (technical term).

The assumptions, a) constant variability about the model, b) normal distribution, c) fitting data and d) no influential or outlaying points, of a non-linear regression, as it has been described here, have been tested against violations. In the plots means and confidence intervals of 95% or median and 25%/75% quartiles are shown. Note that in some areas and years, there were very few or no data. Hence, all data with N < 5 were excluded from graphics and further statistical analyses.

Downloaded receiver logs (vrl files) were initially managed within a VUE data base (Vemco Division, Amirix Systems Inc., Halifax, Canada). The data were downloaded the last time 25/10/2012. For the analyses signals from individual fish to multiple receivers over time were used. In the case of multiple receivers with overlapping detection range the mean position = PAV for every 30 min of monitored herring in the study area were estimated using a mean position algorithm (Simpfendorfer et al., 2002). Three different fates were determined for each individual 1) survival within the study area, 2) natural mortality within the study area and 3) dispersal out of the study area. As long as the signal indicated movements the fish were considered to be alive. When a signal was sent continuously within the selected time interval of the transmitter to the same receiver for some time natural mortality was inferred. It could not be distinguished between a living herring and an eaten herring by predator as long as the signal was moving. But after digestion the predator will excrete the transmitter and can be followed identified as dead herring due to the missing movements. Lastly, dispersal out of the study area was inferred when the last signal was detected by one of receivers at the border to Skagerrak. In addition, some signals of collision were deleted manually. Those signals were generated when two signals from different transmitters reached one receiver at the same time. The signals could be identified either through an unknown ID or the signal was senseless, e.g. the fate of a known individual was identified as dispersal out of the study area at a certain time but after the dispersal a single signal was received inside the system without any other detection. Also a signal of a known ID received before the herring was tagged with the transmitter was deleted. Additionally high and low tide records of Strandfjorden (Kartverket og Meteorologisk institutt (Norwegian Hydrographic Service), www.sehavniva.no) were analyzed to demonstrate their influence on the swimming behavior of tagged herring.

For the analyses of the environmental data the mean temperature and salinity of all 4 depths in Flødevigen, 1 m, 20 m and 75 m along the west coast and and the depth of 0 m, 5 m and 10 m in Landvikvannet were calculated. Data taken in Flødevigen and the west coast were pooled for the spawning season from March until June, while only data from May were used from Landvikvannet. To present inter-annual differences in temperature and salinity graphically, the data were smoothed using 3-year running means, except data from Landvikvannet. But for statistical tests, the actual annual means were used. For environmental data collected in Landvikvannet, data from May were analyzed due to the high number of environmental samples since 1983. Therefore, the comparison of the data was not influenced by low temperature in years where no samples were collected in May, but earlier in the year. Also May was chosen according to the results of high and overlapping spawning activity in May for both areas, LV and EC. The depth of 5 m for Landvikvannet was selected due to the end of the oxygen rich layer, while the depth of 10 m was chosen to guarantee a stable environment without direct influence of sampling time according to temperature by sunlight and to salinity by changing tides or rainfall. Therefore these two depths for Landvikvannet, 19 m and 75 m for Flødevigen and 20 m and 75 m for the west coast stations were also selected as stable environments to compare the influence of temperature and salinity on meristic characters like the number of vertebrae or growth for the individual year classes of herring. In this case growth was defined as mean length for 3 year old herring within a year class. The age of 3 years was chosen according to the age distribution of EC and LV as shown in the following results. This comparison was only done for WC, EC and LV because the environmental data were measured in these areas and the potential spawning of these herring in this area. To test the significance of temperature and salinity the Pearson product-moment correlation coefficient was calculated and tested. In addition to the historical environmental data, the data collected during the spawning season 2012 were compared for differences in temperature, salinity, oxygen and hydrogensulfide concentration for Landvikvannet and the inner part of Strandfjorden.

3 RESULTS

3.1 Scale 1: Comparative analyses of historical biological data from oceanic, coastal and local (Landvikvannet) areas

3.1.1 Population structure and dynamics

A total number of 184 807 herring were analyzed from the years 1970–2012 showing total body lengths ranging from 14.0–40.5 cm with a mean value of 26.97 cm and ages ranging from 2–17 years with a mean value of 3.83 years. There were no significant sex differences in the biological characters analyzed (length, age, vertebral count and stage of maturity) in the data sets from the 6 areas (ANCOVA; p>0.05). Hence, all further analyses in this thesis were carried out with sexes merged. A comparison between the 6 areas demonstrated significant differences in total length, age and vertebral count (Figure 6).

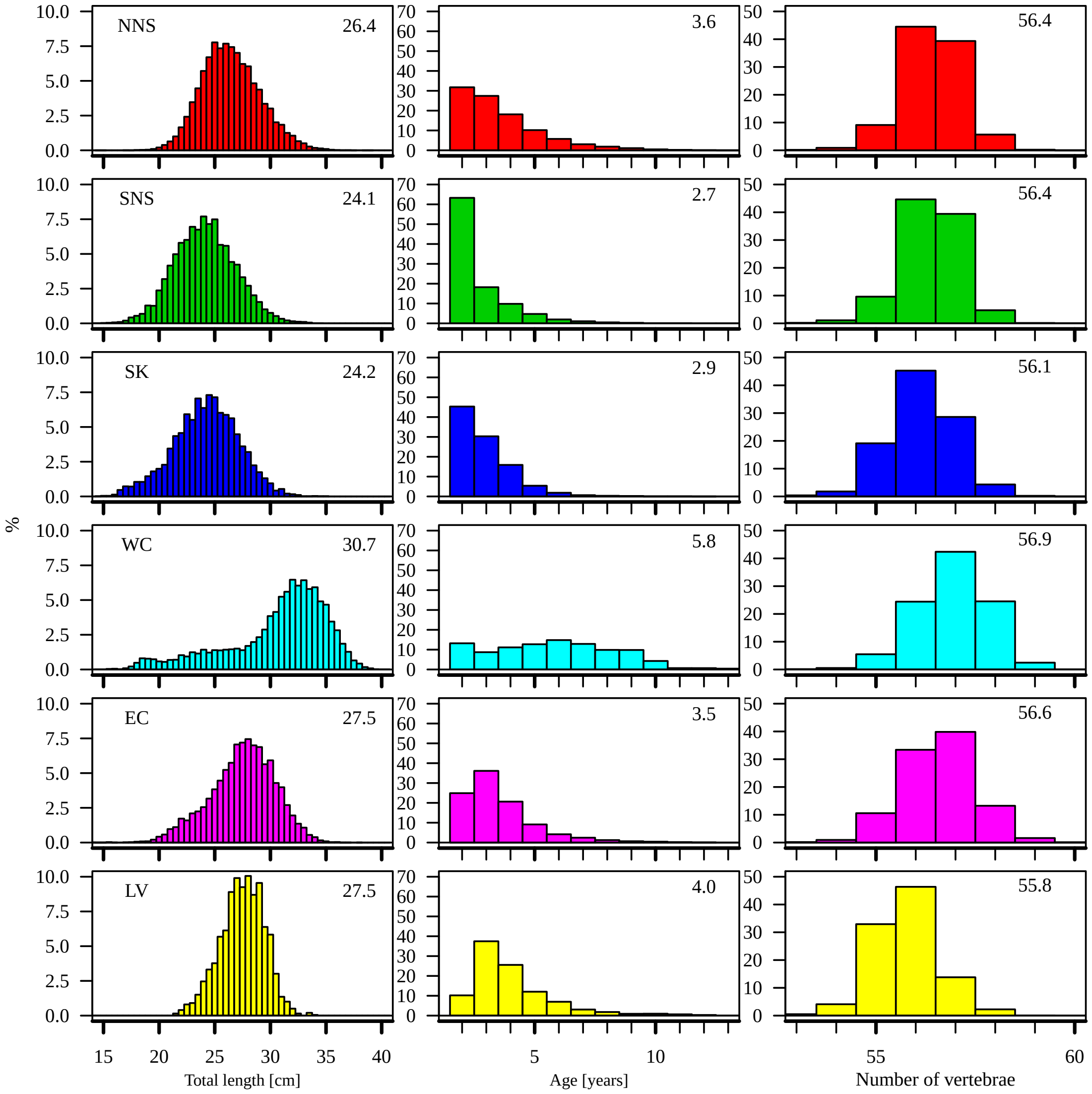

Figure 6: Distribution of total length, age and number of vertebrae by area (data from 1970–2012 pooled) including the mean value for all characters. The range of total length, age and VS was adapted to the amount of herring and therefore negligible amounts were excluded.

Length, age and VS (Kruskal-Wallis and ANOVA; $p<0.001$) were found to differ along areas. Pair wise comparisons between the different areas were also significant for age and length (Mann-Whitney; $p<0.001$), with the exceptions NNS versus EC for age and SNS versus SK as well as EC versus LV for length. VS also differed significantly (T-test; $p<0.001$) for all pair wise comparisons between areas with the exceptions of NNS versus SNS and NNS versus EC. The main tendency was a significant increase in body length and age going from the southern areas SK and SNS towards the north (NNS) and toward the coast (WC, EC and LV), with WC herring being the largest and oldest of all groups. The highest vertebral counts were found at the coast in WC and EC herring. However, inside EC the local group in LV was characterized by the lowest vertebral counts of all 6 groups.

Significant annual variations in age during the period 1970–2012 were found in all areas (Kruskal-Wallis; $p<0.001$) (Figure 7). The largest fluctuations in median age were found in WC where it ranged from 2–10 years. Both in NNS and EC the median aged ranged from 2–6 with a clear peak after year 2000. In LV the time series of median age was not complete, but still a range of 2–5 years and with a peak after year 2000 was apparent. In comparison the median age in SNS and SK was very stable at 2–3 years throughout the study period.

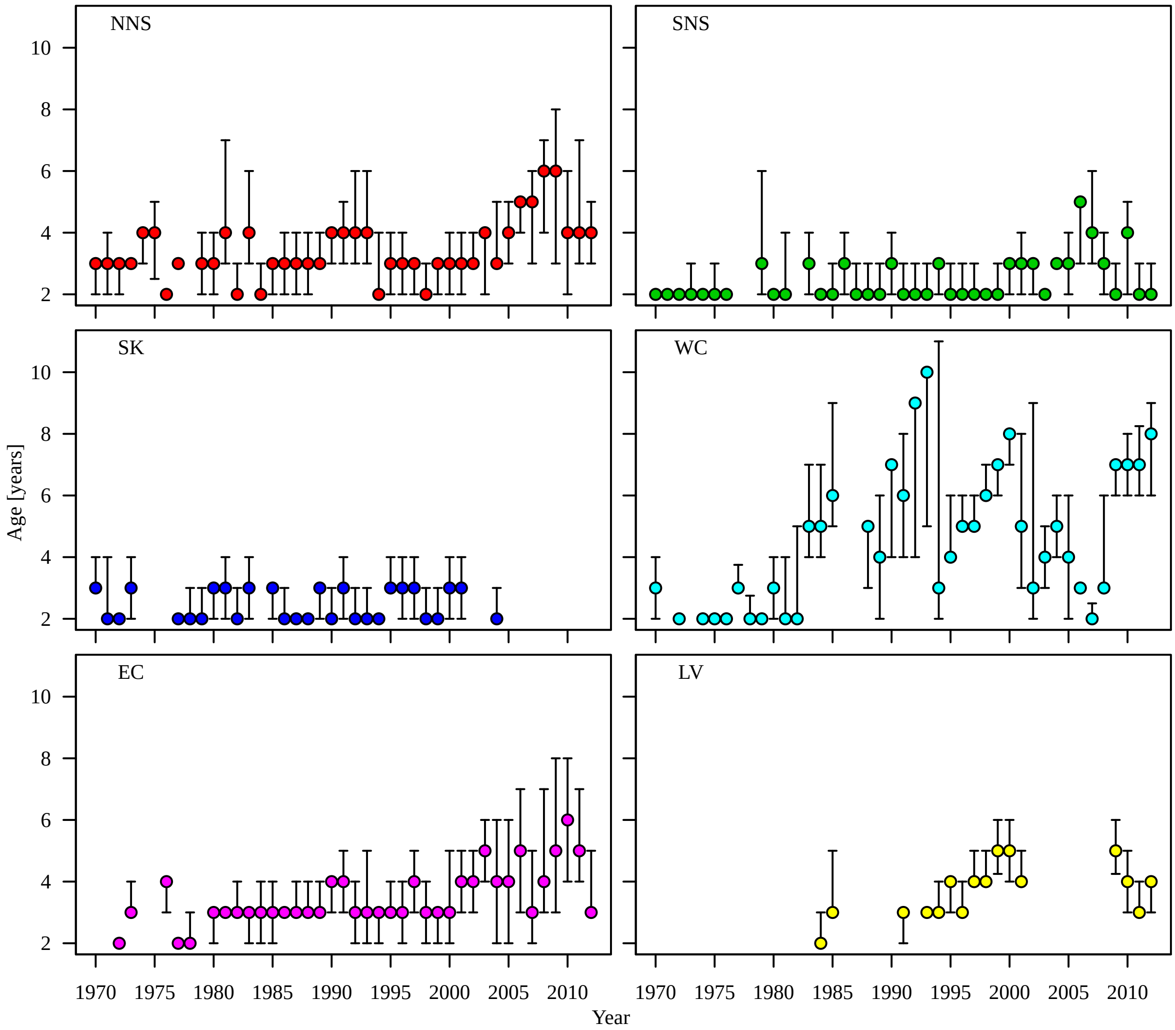

Figure 7: Annual variations in age during 1970–2012 by area (Points = median; T-bars = 25% and 75% quartiles).

The large fluctuations in median age were related to the recruitment of abundant year classes that could be traced in the annual biological samples for many years (Appendix Figure A.1–Appendix Figure A.6). In some areas strong year classes were clearly visible, for other areas year classes were difficult to trace over time. In the NNS area six strong year classes (1970, 1974, 1977, 1986, 1999 and 2001) were visible. Mostly these year classes could be traced for 2 or 3 years, except the year class 1999 and 2001 which could be traced over 6 and 7 years, respectively. The strong 2001 year class was also the only traceable year class in the SNS; else the annual age distributions were with few exceptions always peaking at age 2 years. Also in SK most of the annual age distributions were peaking at age 2 years. Very different than the three oceanic areas was the annual age distribution in WC. Here none of strong NNS year classed could be traced, but the 1983 and 1992 year classes were abundant and visible for the first time in the sampling at the age of 5 years. In the other years there were almost no visible peaks in the WC age distributions, with age groups being present in the same amount and with a higher range than in the other areas. In EC the age distributions seemed to be a mixture of what has been observed in the other areas. Firstly, only one strong year class could be traced, which were the herring hatched in 1998. Secondly, EC could be split into two different historic periods. In the first 3 decades from 1970–1999 the age distribution normally peaked around 3 years and the range of ages was small, whereas in the beginning of the new millennium the 1998 year class appeared, after which the general annual peak of 3 year olds disappeared and the age range increased. The first period was comparable with observations in the oceanic areas, whereas the second period was comparable to observations in WC. In LV no strong year class at all could be traced, and in general there was always a marked peak for 3 or 4 year old herring with a very small age range. Only during two years, 1999 and 2009 the age range was wider and not peaking at age 3 or 4 years.

VS differed significantly with sampling year in all 6 areas (ANOVA; $p<0.001$) (Figure 8), but the range in VS between years and the historical trends in VS varied considerably between areas. The highest range between years was found in WC herring at 1.7 VS. In comparison the range of SNS, SK, EC and LV herring was clearly lower around 1.0 VS, whereas in NNS it was rather stable over the whole period with a range of around 0.4 VS. The historical change in VS followed a similar trend in WC and EC, peaking around 1980, decreasing until around 1990 in EC and 2000 in WC, and peaking again around 2010. A similar trend with increasing VS from 1990s towards 2010 was also apparent in LV, i.e. until year 2000 VS were in most years below the historic mean of the area, whereas from year 2000 onwards VS were above. All in all the increasing trend in LV was the only significant trend along the historical changes in VS (Regression; $p<0.001$). In NNS and SK VS of the 1970s were higher than in the rest of the study period where clear trends were not visible. In SNS no clear trend in VS could be seen over the study period, but VS were highly variable prior to and after a very stable period from 1983-1993.

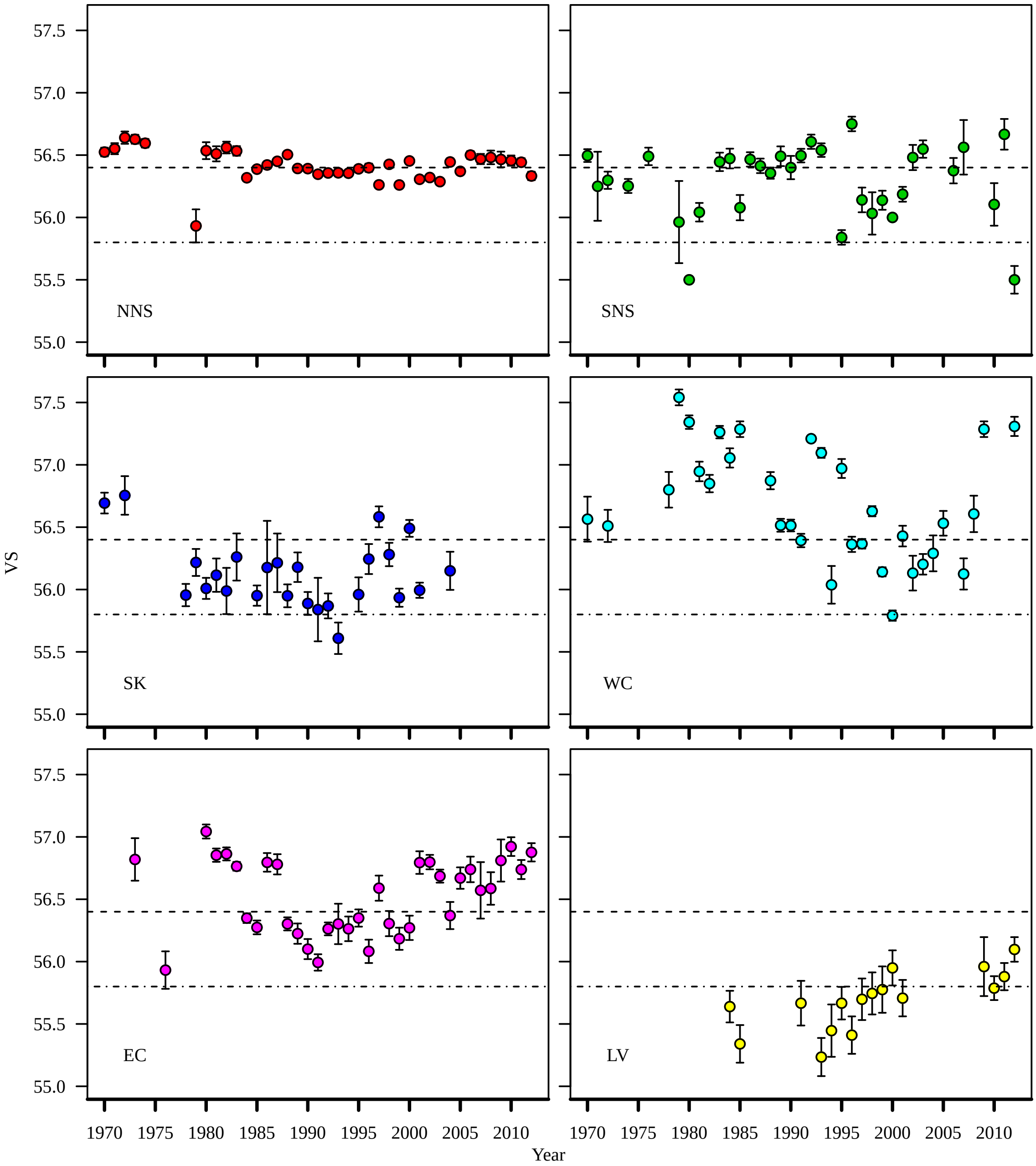

Figure 8: Mean vertebral counts and confidence interval of 95% of herring per year for 6 different regions collected from 1970–2012. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

VS also differed significantly between year classes in all 6 areas (ANOVA; p<0.001) and the observed differences in ranges and historic trends between areas were comparable to that observed between years (Figure 9). In fact the historic trends appeared even clearer for the change in VS by year class as compared with the data with all year classes pooled by year. In the coastal areas WC and EC the VS peaked for year classes born during the mid-1970s and after year 2000. In LV most of the year classes born until 1995 were characterized by VS lower than the historical mean of the area, whereas the VS of most year classes born after this were at or above the historical mean. As seen before the increasing trend in LV was also significant for the year classes (Regression; p<0.001). In NNS and SK the VS of year classes born up to 1970 were higher than in the following year classes, where VS were more stable around the historic mean of the area.

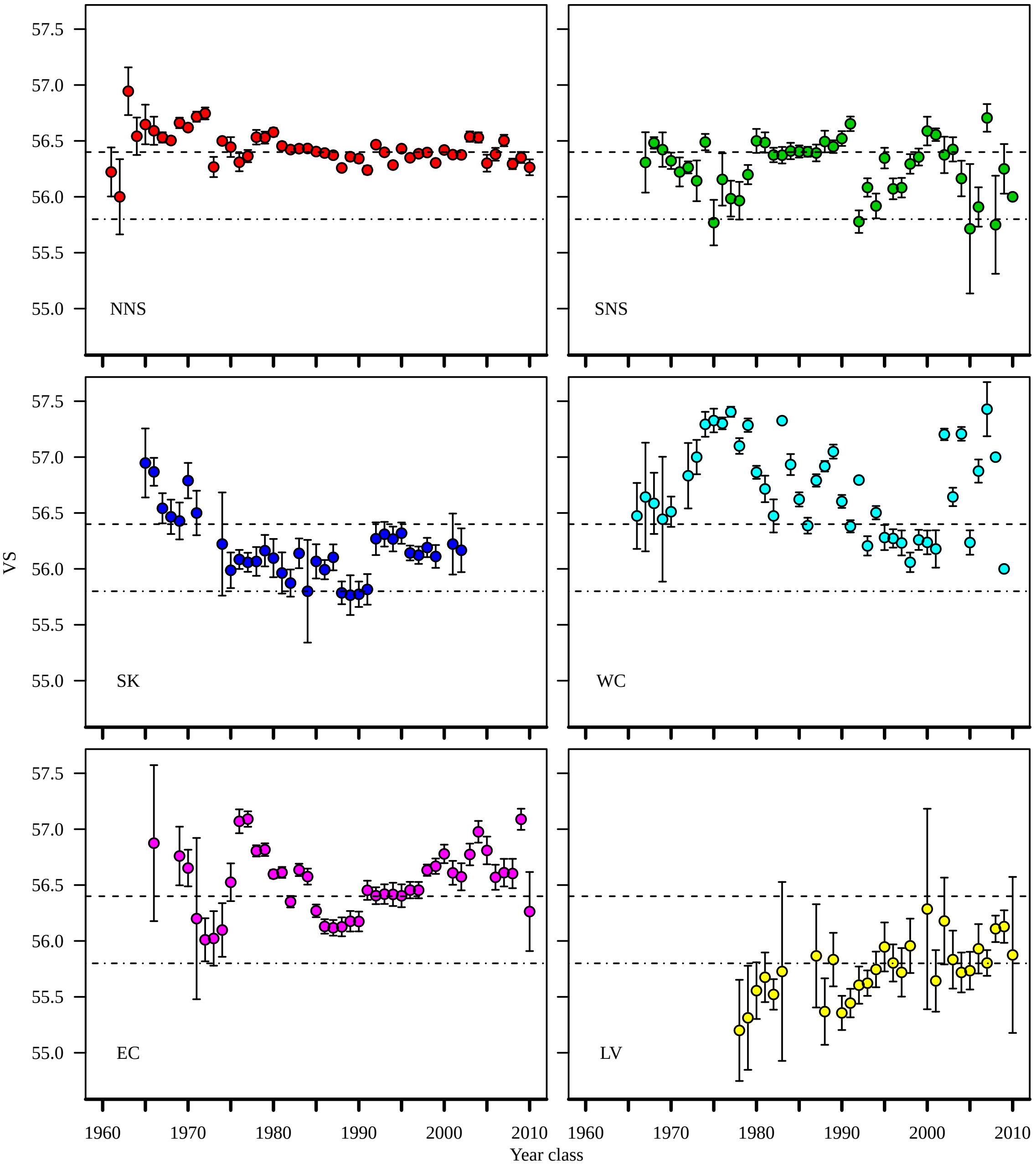

Figure 9: Mean vertebral counts and confidence interval of 95% of the different herring year classes in 6 regions collected from 1970–2012. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

Significant intra-annual variations in VS in data pooled by month were found in all 6 areas (ANOVA; p<0.001) (Figure 10), but the range in variations and seasonal trends varied considerably between areas. In both North Sea areas no clear seasonal trends were observed and the range was very low at 0.4 VS. The largest range in VS and clearest as well as significant trend (Regression; p<0.001) over a year was found in WC, where the VS decreased from January (57.5) until December (56.2) with the exception of June (56.3). In the SK the VS was above 56.5 in the first three months of a year, after which it fluctuated up and down around 56.1 with values in May, August and December being lower than 56.0. High intra-annual variation in VS was also observed in EC, with values peaking above 56.8 in March and August, and reaching levels below 56.0 in May and July. A rapid decrease in VS from March until May was also found in LV from 56.4 down to 55.6, after which the VS stayed below 56.0. The seasonal variation in VS was also analyzed as mean values for each biological sample taken within each month (Figure 11). This analysis demonstrated that samples with high VS also occurred in periods where the mean of the pooled samples indicated very low VS and vice versa. For example in the North Sea areas mean monthly VS appeared rather stable around the historic mean, whereas in July samples with low VS, below 56.0, were found. Also in WC samples with VS below 56.0 were found in July, whereas in SK such samples were common in all months from May–August including November–December. This demonstrates that low VS herring actually were present in all areas during the summer period. Similarly the sample values demonstrated the occurrence of herring with high VS, above 57.0, in March–April in EC, even inside LV in March.

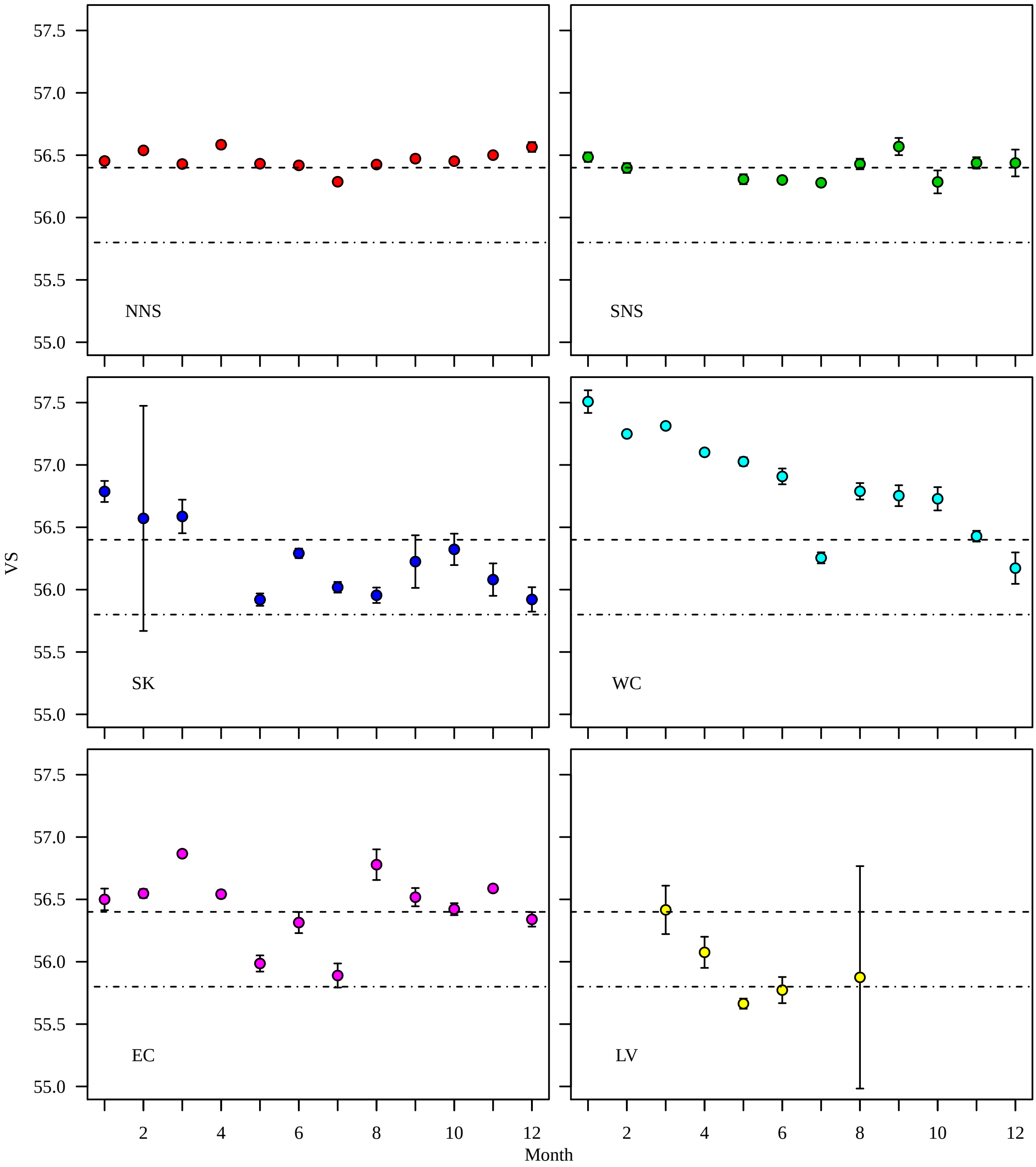

Figure 10: Mean monthly VS and confidence interval of 95% of herring for 6 different regions collected from 1970–2012. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

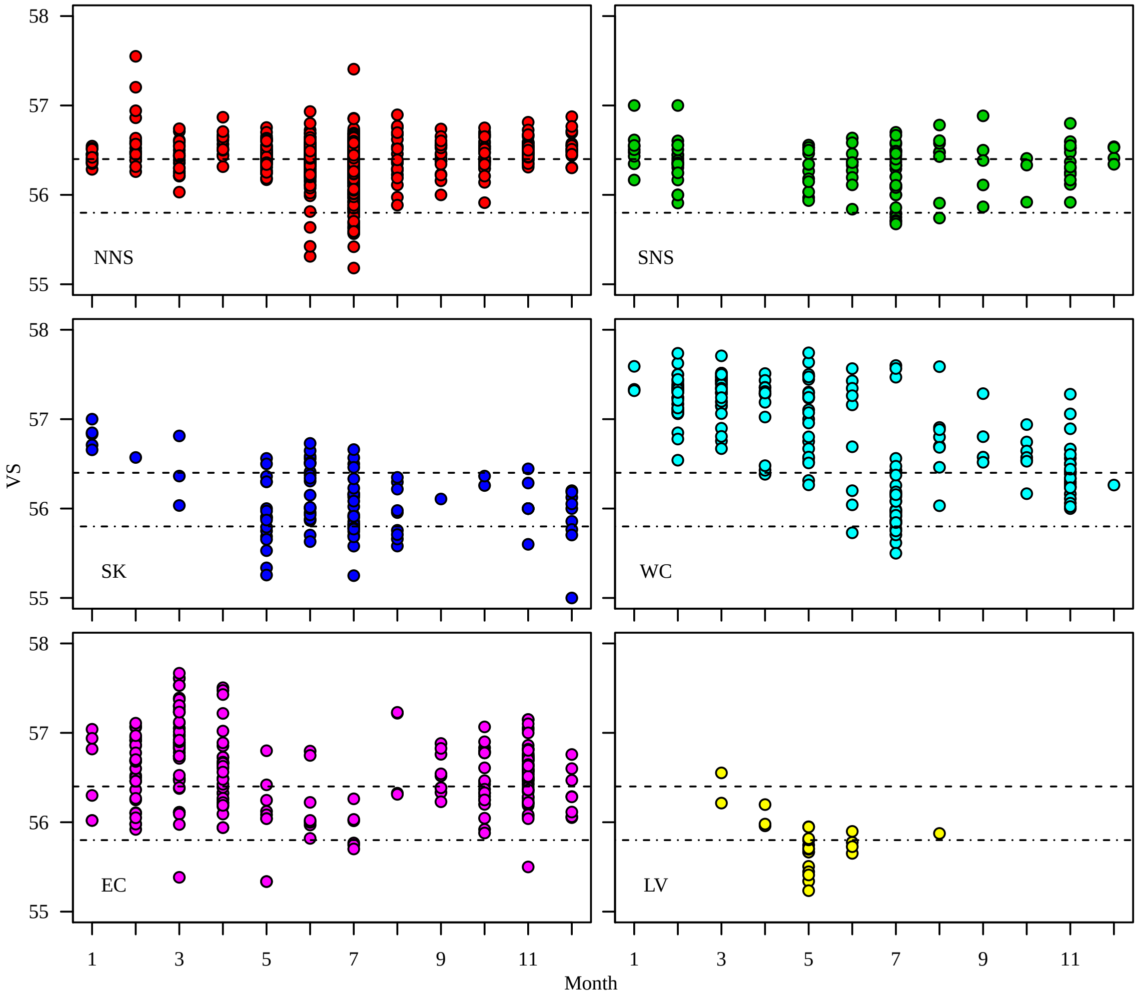

Figure 11: Variation of VS by month and area, values given are mean VS for each sample within a month and area collected from 1970–2012. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

3.1.2 Body growth

The historical length-at-age data showed significant differences between areas (ANOVA: $p < 0.01$) (Figure 12). Coastal herring (WC and EC) were characterized by a higher growth, length-at-age, than the oceanic (NNS, SNS, SK) or local herring (LV). The highest growth was found in WC herring, sticking out not only with high length at age, but also with a high over all maximum age and asymptotic length. Given that the data material was sparse for most ages of 7 years and older in all areas except for WC; the differences found in length between areas in these age groups were not considered in any further details. When focusing on the most abundant ages 2–6 years, the SNS was clearly the one with the slowest growing herring, but also SK herring appeared as slow growers. Length of LV herring at ages 3–5 years was higher than in NNS herring. However, the difference was highest at age 4 years and reduced as the fish grew to be 5 and 6 years, indicating a different pattern of growth. If one only considers length at age 4 years, there was a range of 3 cm from 29.5 cm in WC herring until 26.5 cm in SNS herring, which is a significant gap in herring growth. Periodical changes in growth were demonstrated as significant inter-annual differences in length-at-age for 2–5 year old herring captured between January and

June in all areas (ANOVA; p<0.001) (Figure 13). The inter-annual variation was clearly lowest in NNS. Still, a clear trend in growth was observed with a peak around 1980s and a concurrent decrease until it flattened out after 2000. Such a clear trend in growth could not be found in any of the other areas. In the SNS the mean length fluctuated within a range of 5 cm for all ages. In SK there range of the mean length was even bigger than for SNS, but no pattern at all was visible. The range of mean length for WC herring was smaller than for SNS and SK. Except the years between 2000 and 2005 where the mean length decreased for all ages, there was no clear tendency. Along the EC the range was even smaller than for WC herring of age 3–5 years, and the range of 2 year old herring was as high as seen for SNS herring. Still the increase in mean length at age during 2000 and the following years was visible but not as clear as for WC. In LV the main pattern found was a continuous increase in mean length for age 4 years from 1990–2000.

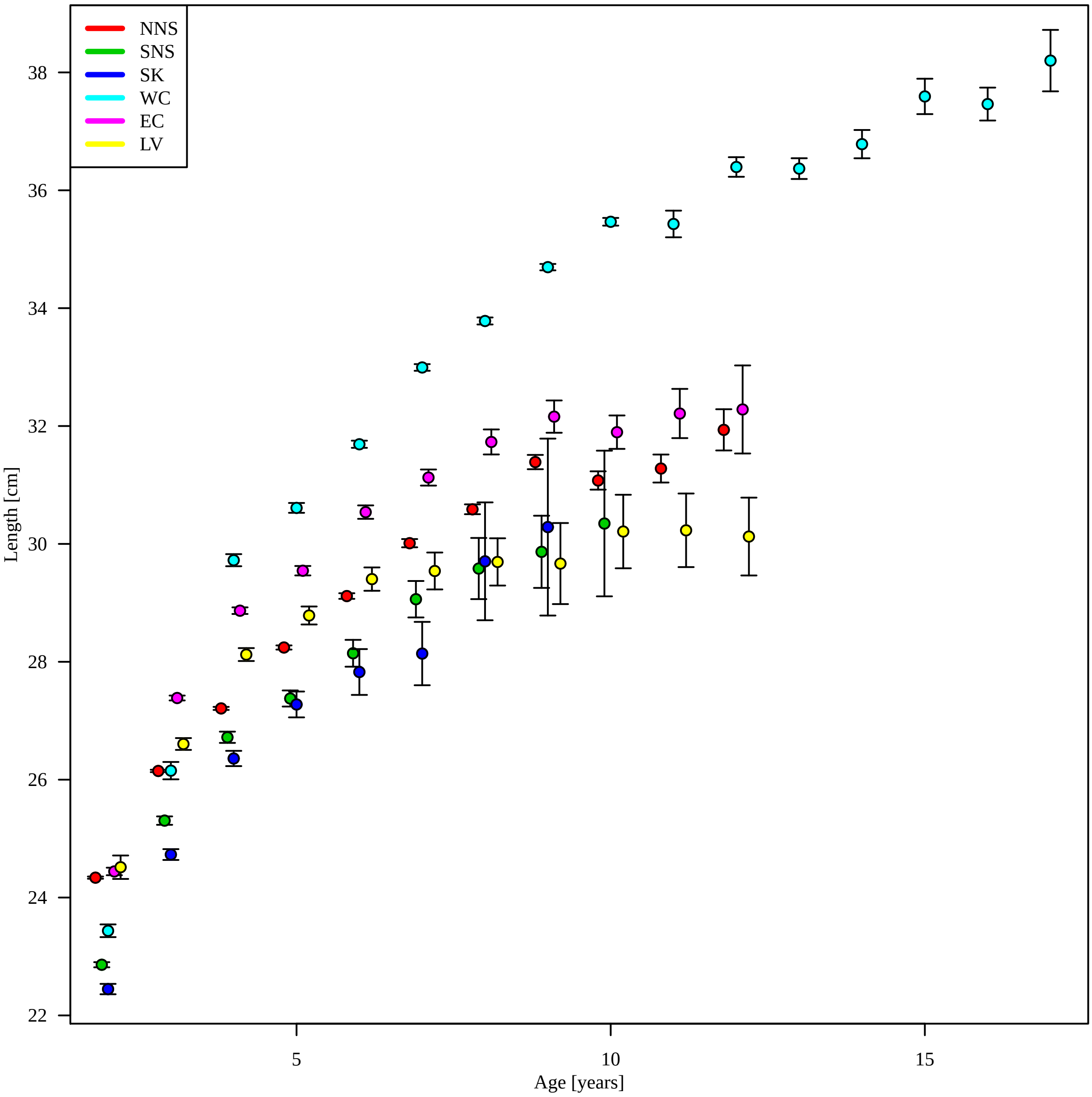

Figure 12: Growth curves (Length-at-age) by area. Points and T-bars show the mean and the confidence interval of 95%.

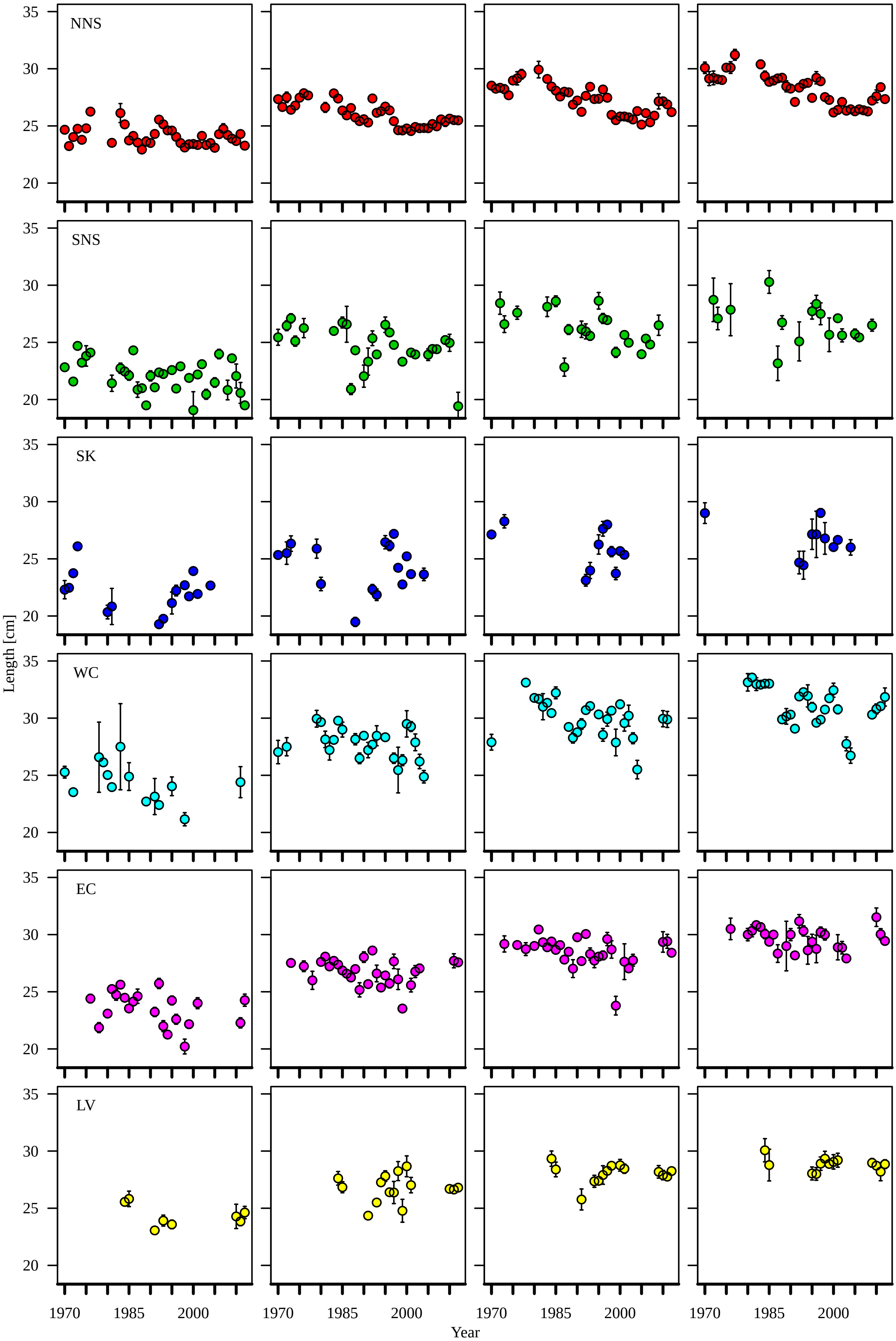

Figure 13: Inter-annual changes in mean length of herring collected from January until June for ages 2–5 by the 6 areas.

3.1.3 Maturation and spawning time

Based on the distribution of maturity stages in herring by area and month, herring from the 6 different areas could be separated into three main groups, the oceanic, coastal or local herring (Figure 14). In the oceanic areas (NNS, SNS, SK) most herring were spent or recovering in the first 6 months, except in the SK area in January and March. From May on more and more herring become maturing peaking in July, and in August and later in the autumn the amount of recovering herring increases rapidly again for both North Sea areas. In the SK maturing herring were abundant throughout September, after which spent and recovering herring predominated. Actual spawning stages were quite rare in the material of the oceanic areas, indicating that the spawning areas have not been properly sampled. However, along the WC, EC and LV, spawning stages were very common in spring. Still the maturity composition of herring appeared to differ between the areas, yet with a clear overlap in spawning stage. In January and February in WC most herring were maturing and ripe. This changed dramatically in March where the spawning clearly took place and some spent herring were already present. Until July most herring were spent or recovering along the WC. The rest of the year only maturing herring were present, with one exception in September and October where spawning and recovering, respectively, herring were present. The first three months along the EC were comparable to that observed in WC, but in EC spawning herring were present throughout June. The number of recovering herring in EC increased until July, but this stage was not as frequent as along the west coast. From September on only maturing and a few ripe herring were present in EC. Maturity stage composition in LV herring was quite similar through all months. From March until May half of the herring present in LV were spawning, whereas the other half was ripe. Only very few spent and recovering herring were present during all sampling months. The change took place in August where only maturing herring were present.

The stage of maturity differed significantly during the year in each area (Kruskal-Wallis; p<0.001), and it differed between areas for each month studied (Kruskal-Wallis; p<0.001). During the

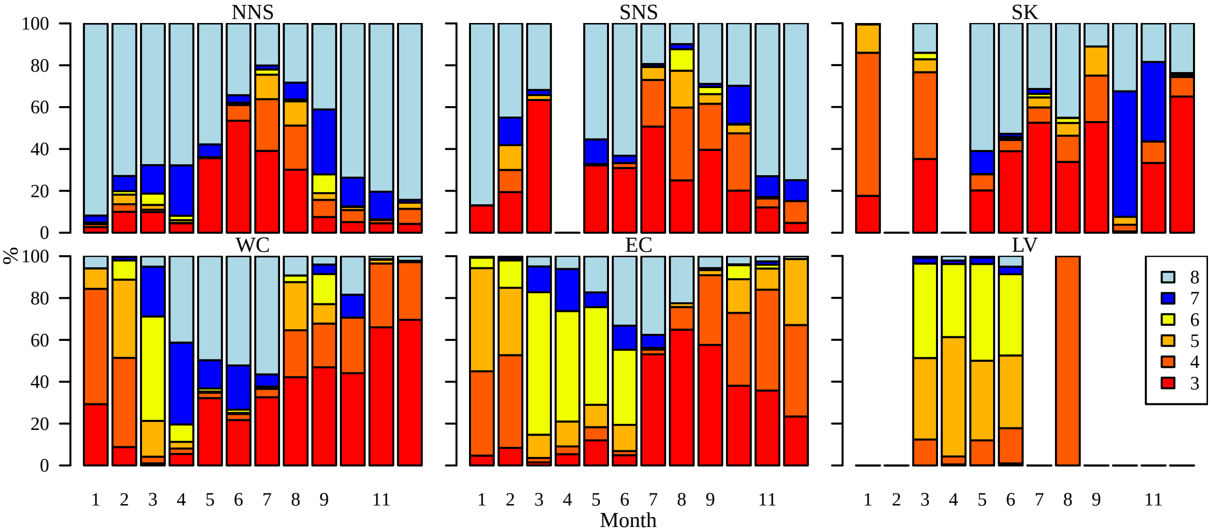

Figure 14: Stage of maturity composition by month along 6 different areas.

spawning period March to June in LV there was no significant difference for the stage of maturity (Kruskal-Wallis; p>0.05). In contrast to LV herring, the stage of maturity was found to differ significantly from March to June in EC (Kruskal-Wallis; p<0.001).

A decadal comparison of maturity stage composition from March–June for the two coastal areas (EC, WC) and LV demonstrated historical changes in maturation and spawning activities (Figure 15). Along the WC the proportion of spawning individuals in March and April decreased from the 1980s until present time, where a high proportion of post-spawning stages indicated that spawning mainly took place in February. Along the EC caught herring during the periods 1980s and 2000s were comparable with regard to the maturity stage composition from March–June, with spawning occurring in all months. However there was a tendency that herring were less mature and spawning occurred later in the 2000s than in the 1980s. The period 1990s were totally different from the 1980s and 2000s, with spent and recovering herring being more frequent in March and April and spawning herring were absent from the samples in May–June. Also in LV a

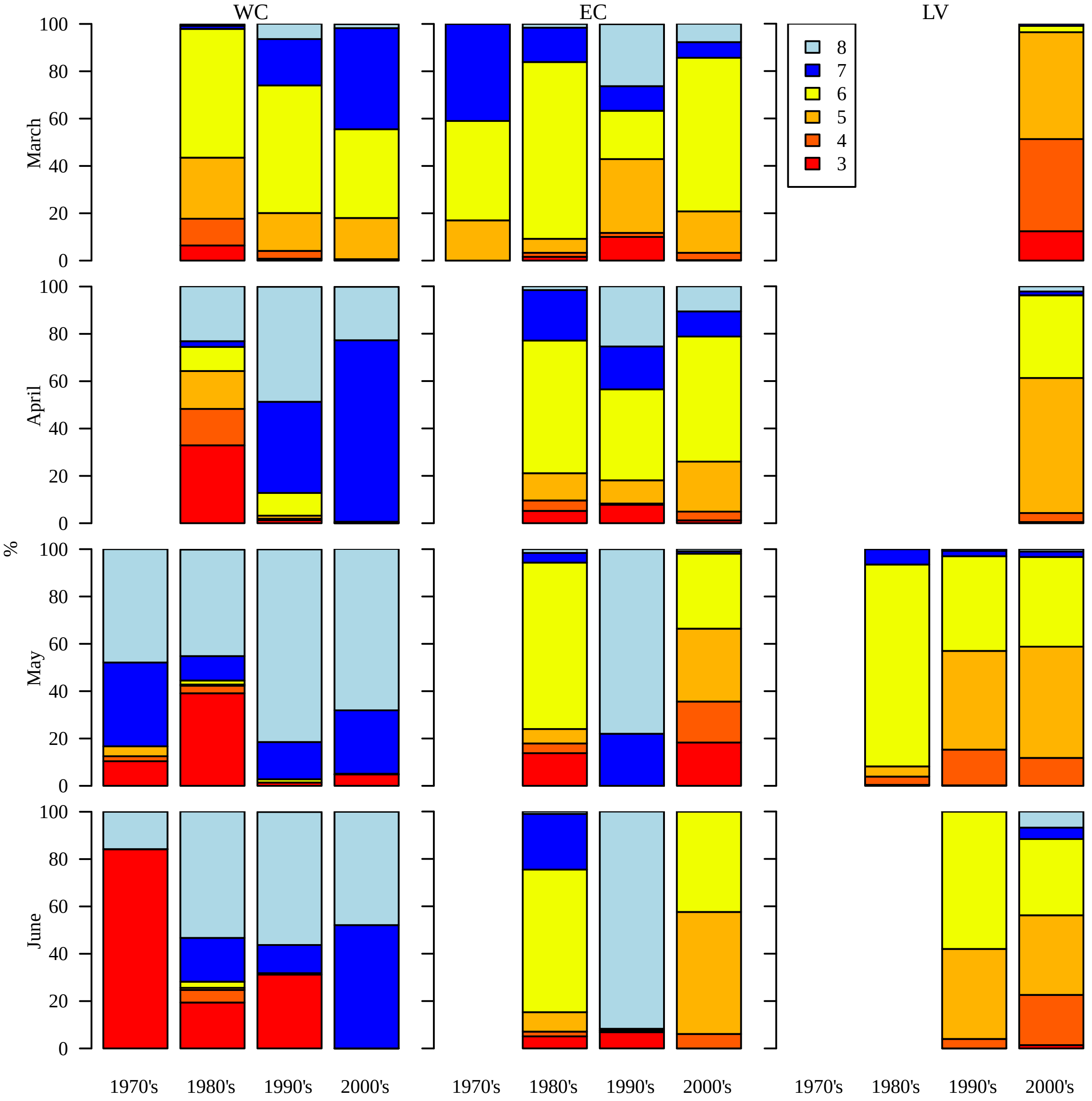

Figure 15: Changes in stage of maturity composition by decade and areas for the months March-June.

change in maturation and spawning took place during the last 30 years; in the 1980s more than 80% were in a spawning stage in May, whereas in the 1990s and 2000s less than 40% were in a spawning stage in May and instead the maturing herring predominated leading to a prolonged spawning period.

3.2 Scale 2: Analyses of biological data during the 2012 spawning season in Landvikvannet and connected fjords

3.2.1 Population structure and dynamics

A total number of 1 260 herring were analyzed during the spawning season in 2012 showing total body lengths ranging from 22.0–34.5 cm with a mean value of 28.26 cm and ages ranging from 2–12 years with a mean value of 4.24 years (Figure 16). Within collected OLV and ILV herring NSS herring could be identified as a known herring population due to otoliths characters and their high vertebrae counts. NSS herring were captured in both ecosystems but were more present in the connected fjords (73.1%) than in Landvikvannet (26.9%). There were no significant sex differences in the biological characters analyzed (length, age, vertebral count and stage of maturity) for OLV and ILV herring and typed NSS herring (ANCOVA; p>0.05).

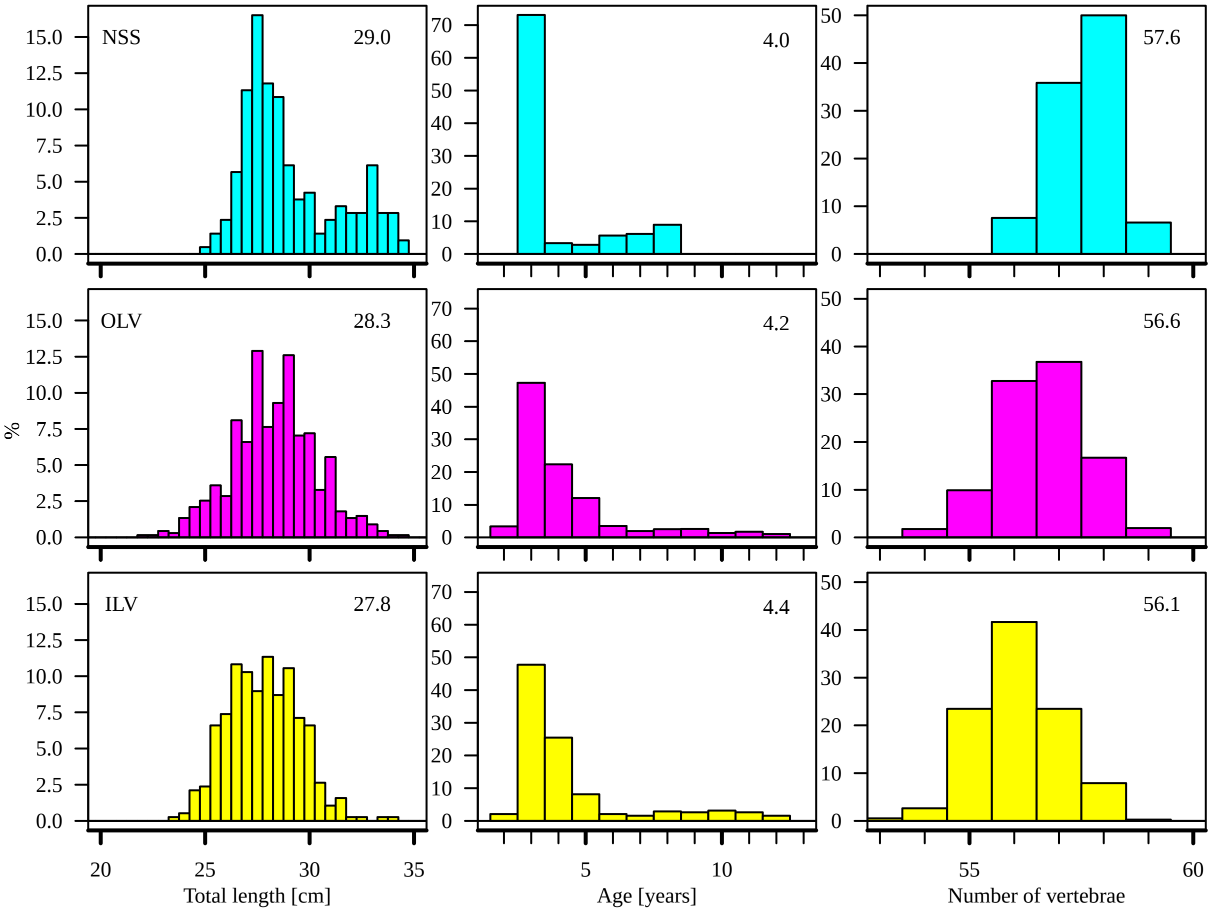

Figure 16: Distribution of total length, age and number of vertebrae for herring typed as NSS, OLV and ILV in the detailed spawning season of 2012, including the mean for each character. The range of total length, age and VS was adapted to the amount of herring and therefore negligible amounts were excluded.

Hence, all further analyses were carried out with sexes merged. A comparison between the 3 herring types demonstrated significant differences in total length, age and VS. Length, age and VS (Kruskal-Wallis and ANOVA, $p<0.001$) were found to differ between NSS, ILV and OLV herring. Pair wise comparisons between the different types were also significant for age and length (Mann-Whitney; $p<0.001$), with the exception of OLV versus ILV for age (Mann-Whitney; $p>0.05$). VS also differed significantly (T-test; $p<0.001$) for all pair wise comparisons between types without any exceptions. The main tendency was a significant increase in body length and VS from ILV, OLV to NSS, while the age decreased.

During the spawning season the occurrence of the 3 herring types (adjusted to sampling effort) differed considerably (Figure 17a). ILV herring entered Landvikvannet in the beginning of March and left again between June and August (only 10 herring were caught in August). In the connected fjords OLV herring entered and left the area earlier, in February and May–June, respectively. NSS herring left the study area even earlier (in May) than OLV and ILV herring. While NSS and ILV had a peak occurrence in the samples around 26/3 and 14/5, respectively, OLV were most abundant in all samples during March. Almost none ILV were collected in February, beginning of March and August. Also less OLV and NSS were collected in February. NSS were present the last time in May, while OLV were also present in June, but both were absent in August. OLV dominated the composition of different herring types in February

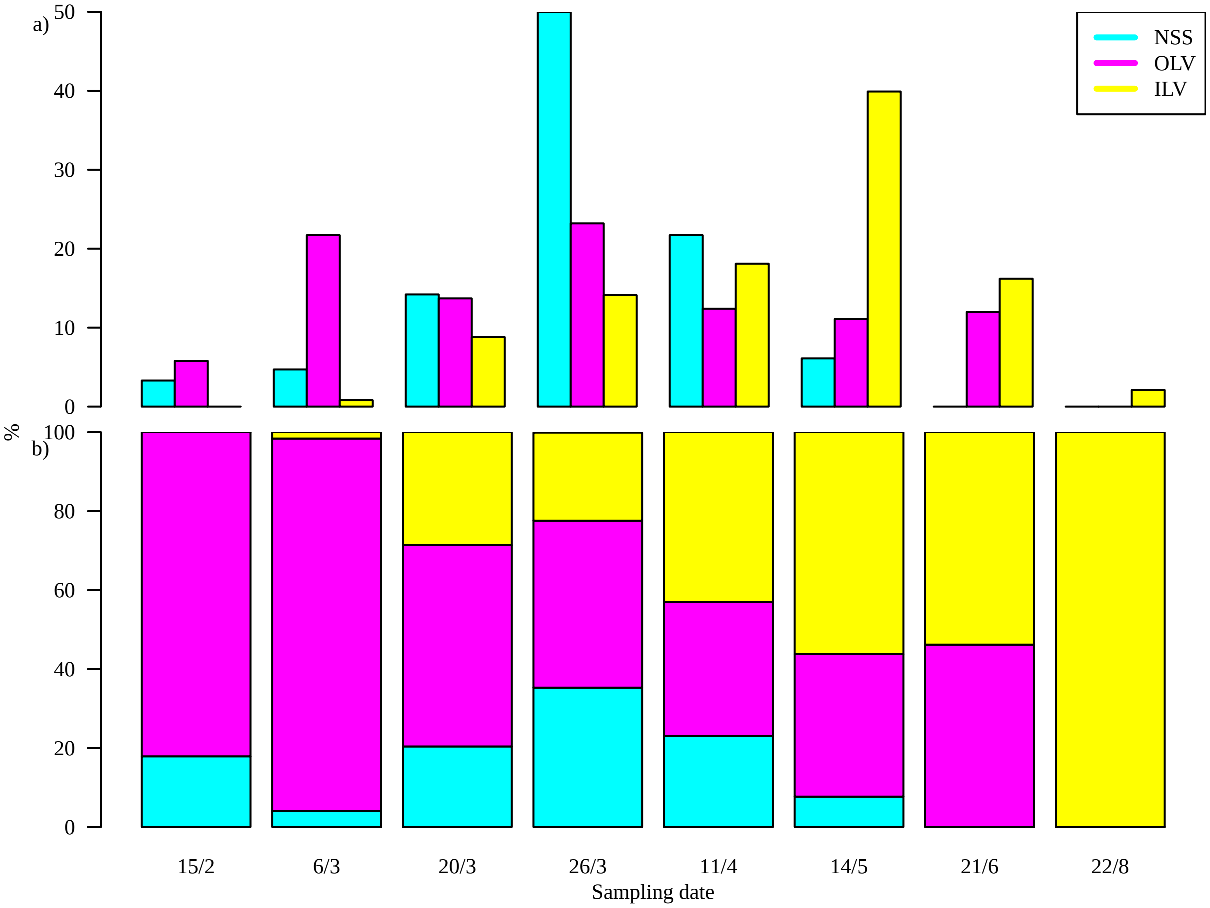

Figure 17: a) proportion of herring typed as NSS, OLV and ILV at a sampling date relative to total abundance of the specific type in the catches over the entire season and b) catch composition in regard to herring types for each sampling date.

and the beginning of March (Figure 17b). The dominance was broken in March and April when NSS, OLV and ILV were relative equally abundant. After the disappearance of NSS more than 50% of the herring were ILV in May and June, to the point of a total dominance by ILV in August. In addition to herring some predators, mostly cod, with empty stomachs were caught as well in the connected fjords. Only predators captured in June had full stomachs, but exclusively shrimps. In contrast to the connected fjords almost no predators were caught in Landvikvannet. Just some saithe (*Pollachius virens*) were caught in June (n = 3) and August (n = 2) with empty and full of shrimps stomachs, respectively. Beside the saithe a few mackerels (*Scomber scombrus*) (n = 4) were caught in Landvikvannet during June. Predators were caught by chance in gillnets without any special effort on predators.

Total length, age and VS varied significantly (Kruskal-Wallis and ANOVA; p<0.001) over the detailed 2012 sampling season in OLV and ILV herring, but not in NSS herring (Figure 18). These changes followed a clear trend where length, age and VS increased and reached their maximum in the sample 26/3, followed by a constant decrease until June for OLV and May for ILV. The decreasing trend of length and VS was significant for OLV as well as for the VS of ILV (Regression; p<0.05). After the majority of ILV herring left in May, total length and age increased again in June and August, whereas the VS in both ILV and OLV continued to decrease

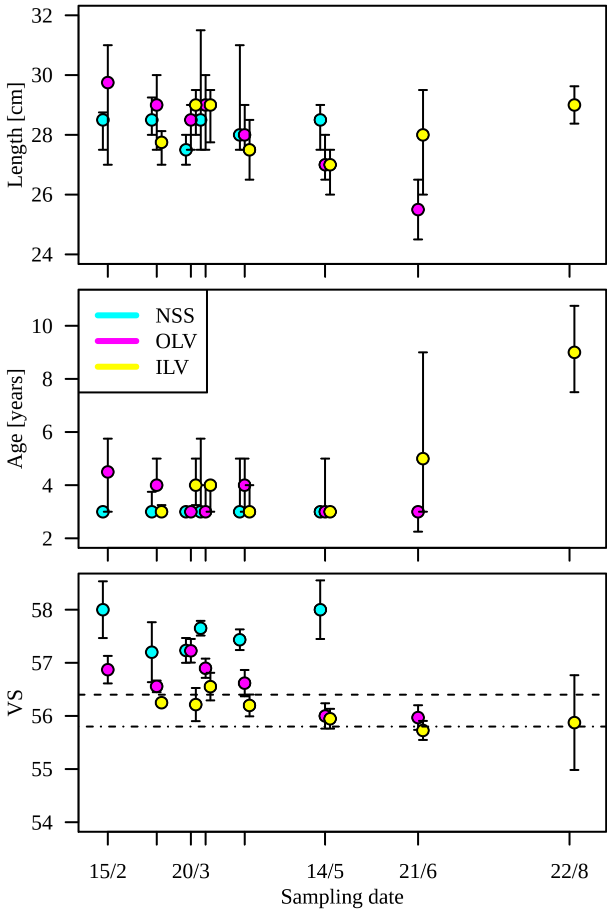

Figure 18: Changes in total length, age and VS by date for herring typed as NSS, OLV and ILV. Median and 25%/75% quartiles are given for length and age, whereas mean and confidence interval of 95% for VS. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

and dropped to historical Landvikvannet levels.

Besides variations over the season, the VS also changed with age and length (Figure 19). The VS of NSS herring did not differ significantly with age or length. In OLV and ILV the VS fluctuated significantly with age (ANOVA; $p<0.05$) without any visible pattern. Quite high VS were found for 3 year old OLV herring as well as ILV herring. For VS at different lengths the picture was different, with VS differing significantly (ANOVA; $p<0.001$) with a clear and significant increasing trend for ILV and OLV (Regression; $p<0.001$). This trend was even more obvious when relating VS to length within ages 3 and 4 years (Figure 20). In both 3 and 4 year old OLV and ILV herring VS increased significantly with length (ANOVA; age 3: $p<0.001$; age 4: $p<0.05$), whereas in NSS herring no significant difference was found. Also differences in VS between sampling dates were not significant for NSS herring at ages 3 or 4 years, whereas this was the case in both OLV and ILV herring (ANOVA; age 3: $p<0.001$; age 4: $p<0.05$). The decreasing tendency of VS during the spawning season 2012 for OLV and ILV was only significant for OLV at ages 3 and 4 years (Regression; $p<0.05$).

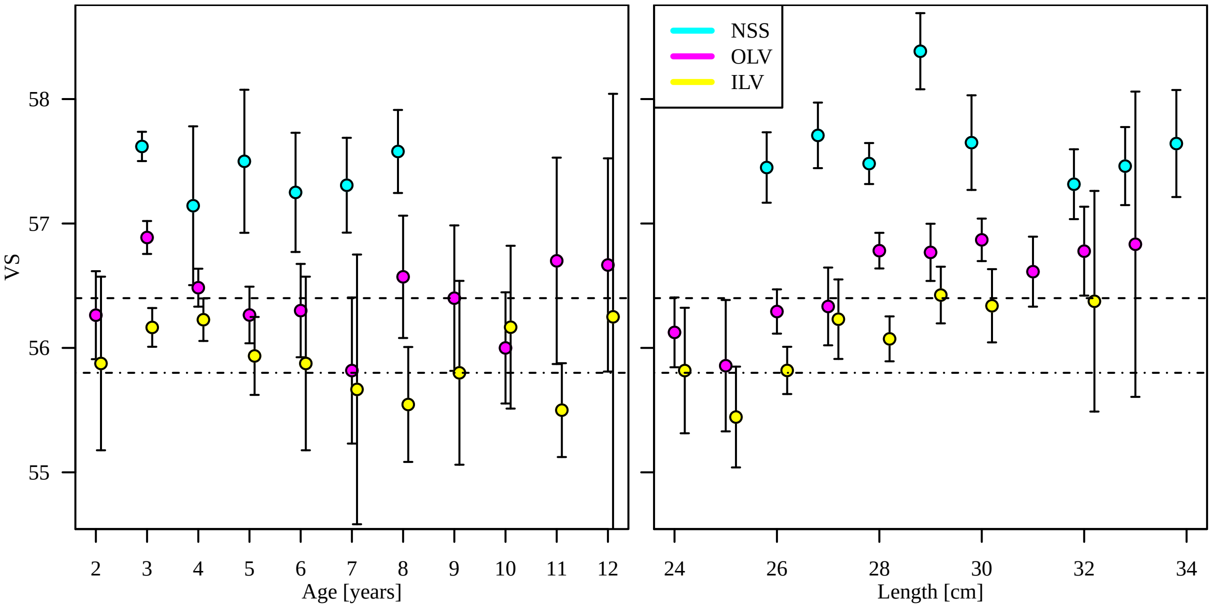

Figure 19: Changes in VS related to age and total length for herring typed as NSS, OLV and ILV. Mean and confidence interval of 95% are given. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

3.2.2 Body growth

Length-at-age data from 2012 demonstrated a significant lower growth for OLV than ILV herring (ANOVA; $p<0.01$), whereas the growth of NSS herring was even higher than in OLV herring (Figure 21). Also fitting the data from 2012 to the von Bertalanffy growth model supported this growth differences (Table 6). From an overall perspective, the data could be sorted into three categories: ‘high growth rate’ (NSS herring), ‘moderate growth rate’ (OLV herring) and ‘low growth rate’ (ILV herring).

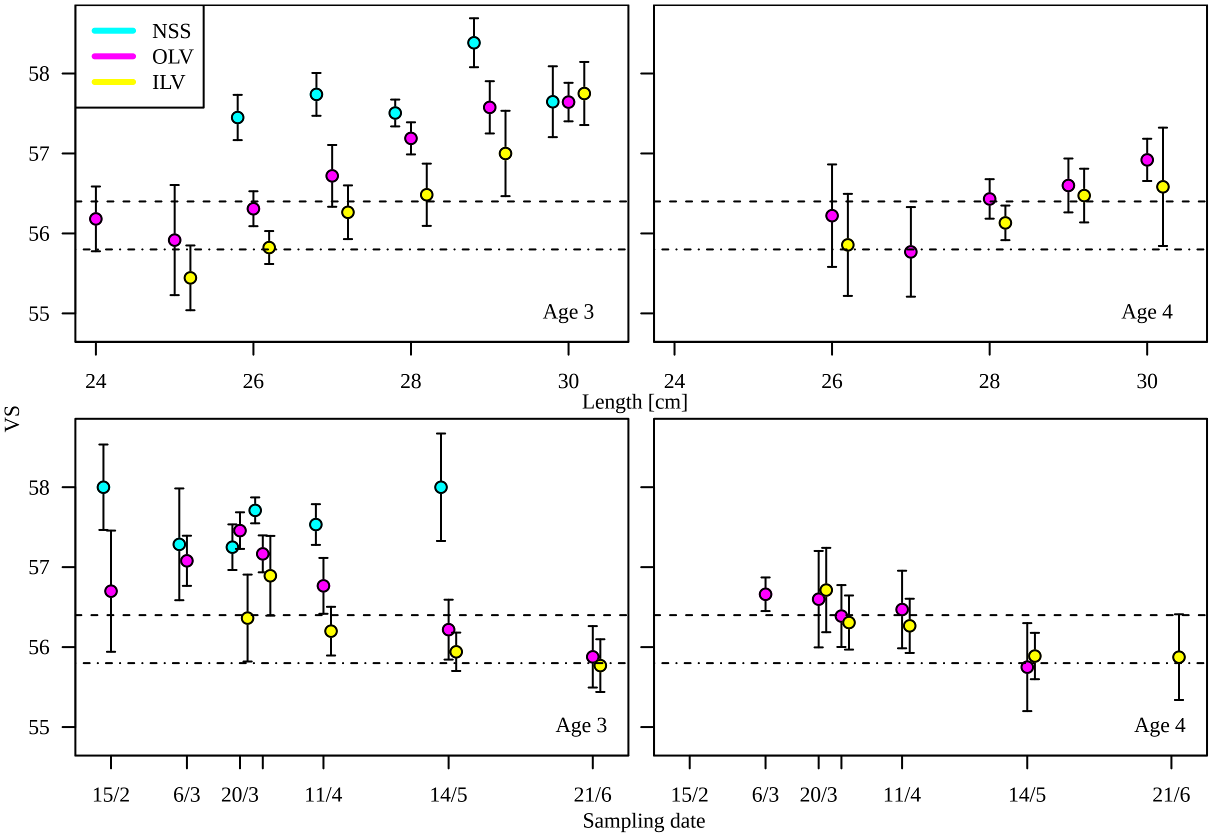

Figure 20: Change in VS by total length and sampling date for age 3 and 4 years herring typed as NSS, OLV and ILV for the spawning season in 2012. Mean and confidence interval of 95% are given. For VS the historical levels from May inside Landvikvannet (dotdashed line) and in the North Sea (dashed line) are given for comparison.

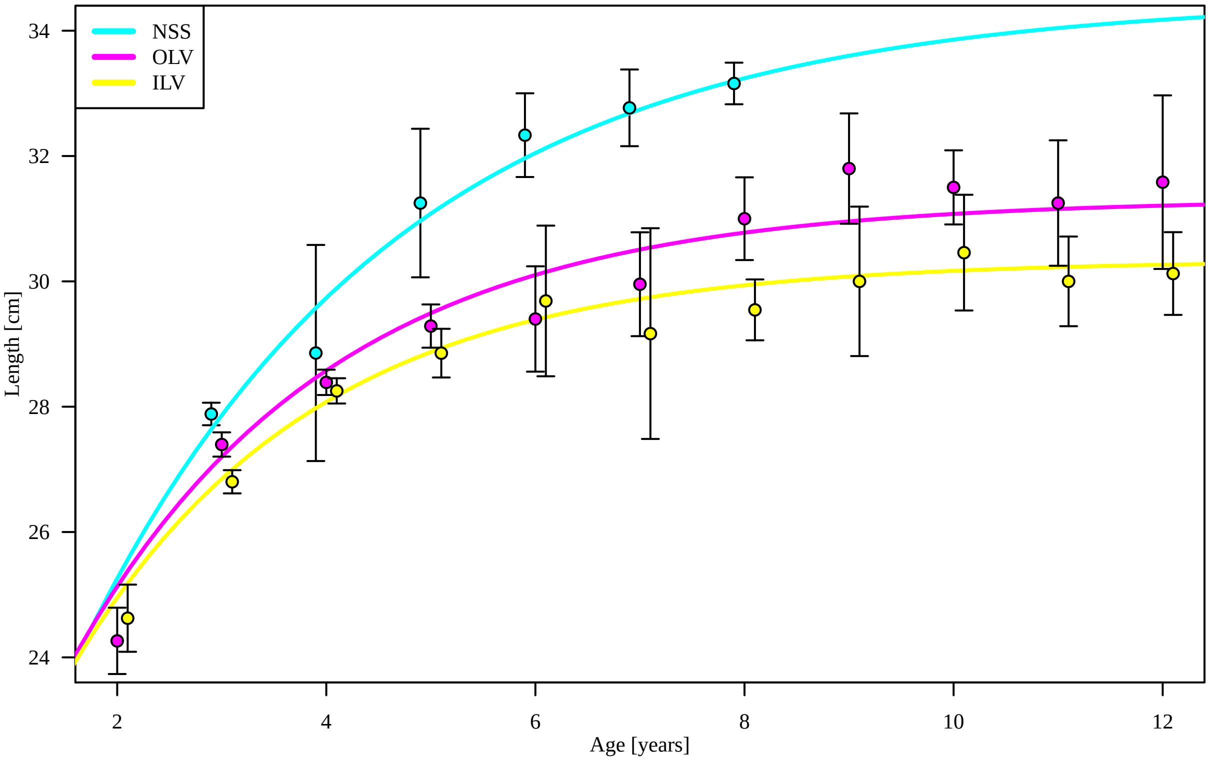

Figure 21: Growth curves (Length-at-age) for data from 2012 by herring typed as NSS, OLV and ILV. Points and T-bars show the mean and the confidence interval of 95%, lines show fitted data to von Bertalanffy growth model.

Table 6: Von Bertalanffy growth parameters of herring typed as NSS, OLV and ILV (L_∞, k, and t_0) from data of annual mean lengths at age in 2012.

	L_∞	K	t_0
NSS	34.5	0.3	-2.0
OLV	31.3	0.4	-2.0
ILV	30.3	0.4	-2.0

In addition, the differences in growth between the three herring types were found when analyzed in different months (ANOVA; p<0.001) (Figure 22 and Table 7). For ILV as well as OLV herring the growth decreased constantly during the spawning season in 2012 (ANOVA; p<0.001). On the other hand, NSS herring did not show any significant change in growth over the sampling season.

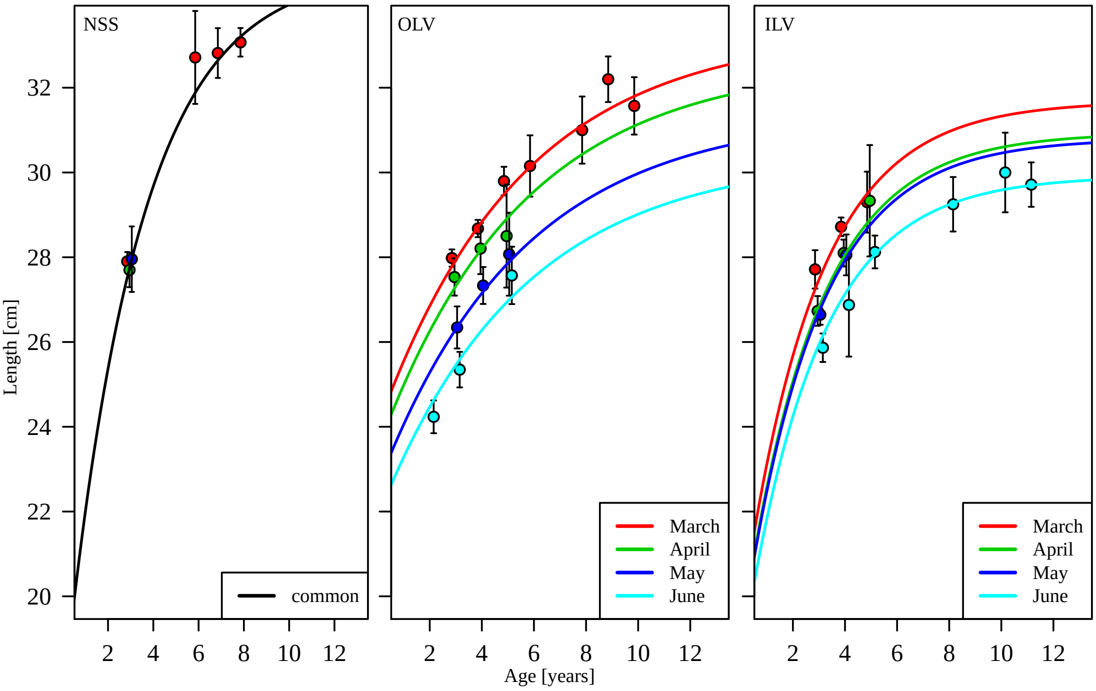

Figure 22: Growth curves (Length-at-age) for different months by herring typed as NSS, OLV and ILV. Points and T-bars show the mean and the confidence interval of 95%.

Table 7: Von Bertalanffy growth parameters of herring typed as NSS, OLV and ILV (L_∞, k, and t_0) from data of annual mean lengths at age for the different months in 2012.

	L_∞	K	t_0
NSS			
common	34.8	0.3	-2.3
OLV			
March	33.4	0.2	-7.0
April	32.6	0.2	-7.0
May	31.4	0.2	-7.0
June	30.4	0.2	-7.0
ILV			
March	31.7	0.4	-2.7
April	30.9	0.4	-2.7
May	30.8	0.4	-2.7
June	29.9	0.4	-2.7

The growth of the herring also differed between herring with different VS and maturation status (ANOVA; p<0.001). Growth increased with increasing VS (Figure 23a and Table 8) and increasing maturation status (Figure 23b and Table 8).

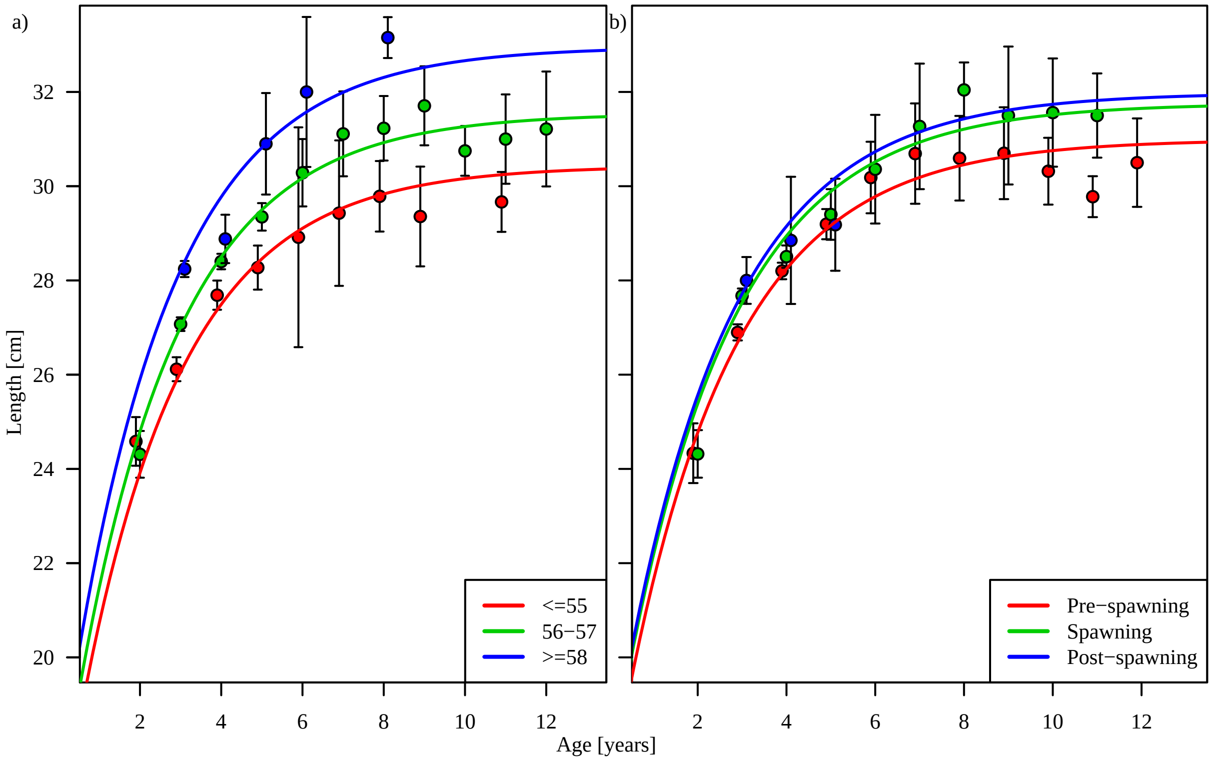

Figure 23: Growth curves (Length-at-age) for herring collected in 2012 by a) vertebral groups and b) maturation status. Points and T-bars show the mean and the confidence interval of 95%.

Table 8: Von Bertalanffy growth parameters of herring pooled into vertebral groups and by their maturation status (L_∞, k, and t_0) from data of annual mean lengths at age in 2012.

	L_∞	K	t_0
VS			
<=55	30.4	0.4	-1.9
56-57	31.6	0.4	-1.9
>=58	33.0	0.4	-1.9
Stage of maturity			
pre-spawning	31.0	0.4	-1.9
spawning	31.8	0.4	-1.9
post-spawning	32.0	0.4	-1.9

3.2.3 Maturation and spawning time

During the spawning season 2012 both pre- and post-spawning as well as spawning herring were present for ILV, OLV and NSS (Figure 24a). Additionally there was an overlap of spawning herring from the end of March until May for all herring, whereas most spawning herring were present at the end of March. Pre-spawning OLV herring were constantly present during the total period, while post-spawning herring were most abundant at the end of March. For NSS most pre- and post-spawning herring were present at the end of March and post-spawning additionally in April. ILV pre- and post-spawning herring were most abundant in March and June, respectively.

While ILV were most abundant along the three groups for pre-spawning herring, they were less abundant for spawning herring (Figure 24b). NSS herring were peaking in the end of March for all spawning conditions. The composition also demonstrated an increasing number of ILV for all spawning conditions within the year.

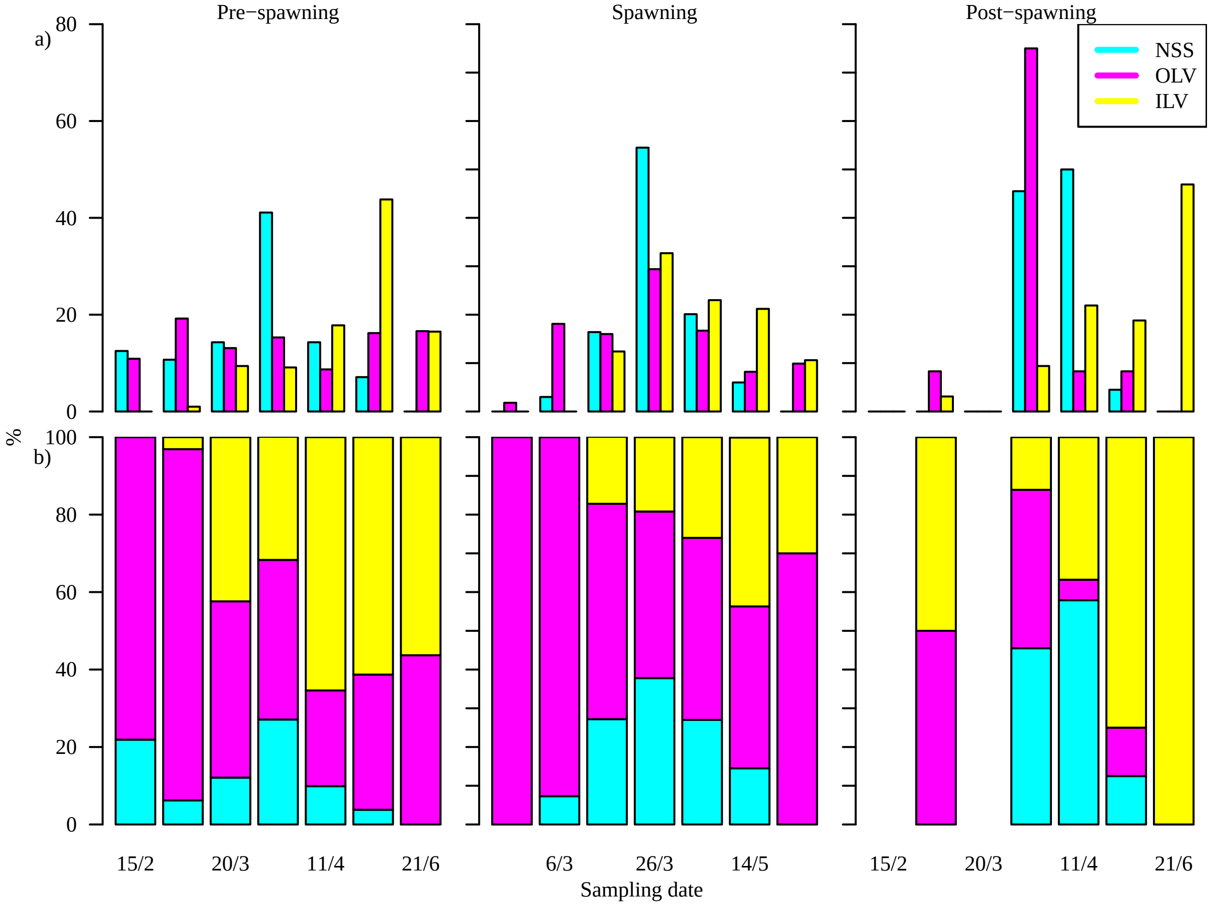

Figure 24: a) proportion of herring typed as NSS, OLV and ILV in regard to their maturation status at a sampling date relative to total abundance of the specific type in the catches over the entire season and b) stage of maturity composition in regard to herring types for each sampling date.

To get a more precise identification of the overlap in spawning between ILV, OLV and NSS, the composition of maturity was separated into pooled length groups (Figure 25). While the maturity was constant for NSS (Kruskal-Wallis; p>0.05), it differed significantly with length for ILV and OLV (Kruskal-Wallis; p<0.001). Thereby the maturity increased significantly with increasing length for both, ILV and OLV (Spearman; p<0.001). Additionally, all NSS length groups existed mostly of spawning herring, only few pre-spawners were present in all length classes. Post-spawning herring were more abundant in NSS for length groups >32 cm. For OLV almost half of the individuals per length group were spawning, with an increasing proportion with increasing length. Also post-spawning herring were almost exclusively present in length groups >32 cm. Spawning ILV herring were not as frequent as for NSS or OLV; about 20% of each length group were in this stage. However, the maturity of ILV also increased with increasing length. Most of the individuals in length groups >32 cm were in a spawning stage. For ILV post-spawning herring were found also in length groups <30 cm. The same effect could be demonstrated with vertebral groups instead of length groups (Figure 26). The maturity differed significantly with VS in OLV and ILV herring (Kruskal-Wallis; p<0.001), but not in NSS herring. Also for VS the maturity increased significantly with increasing VS for OLV as well as ILV (Spearman; p<0.001). Even the maturity of NSS increased with VS but this change was not significant.

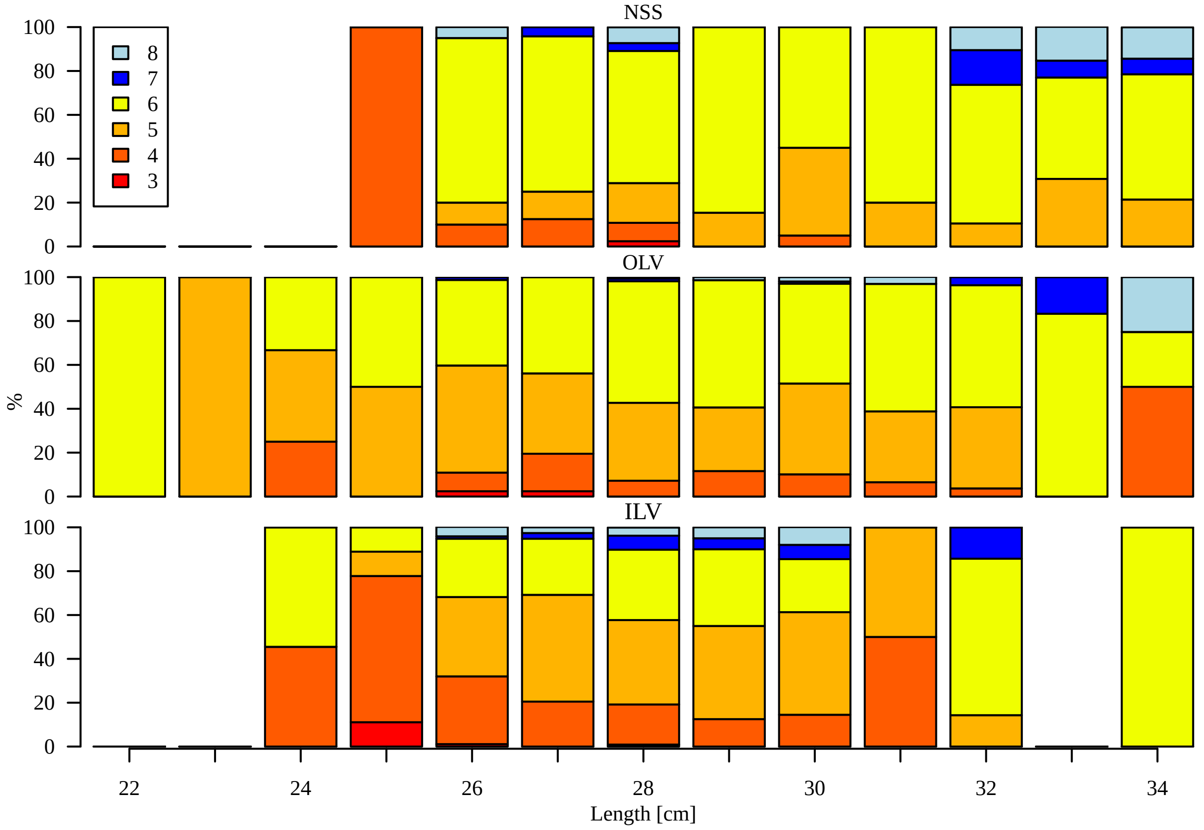

Figure 25: Stage of maturity composition for length classes (pooled to 1cm groups) for herring typed as NSS, OLV and ILV in the spawning season 2012.

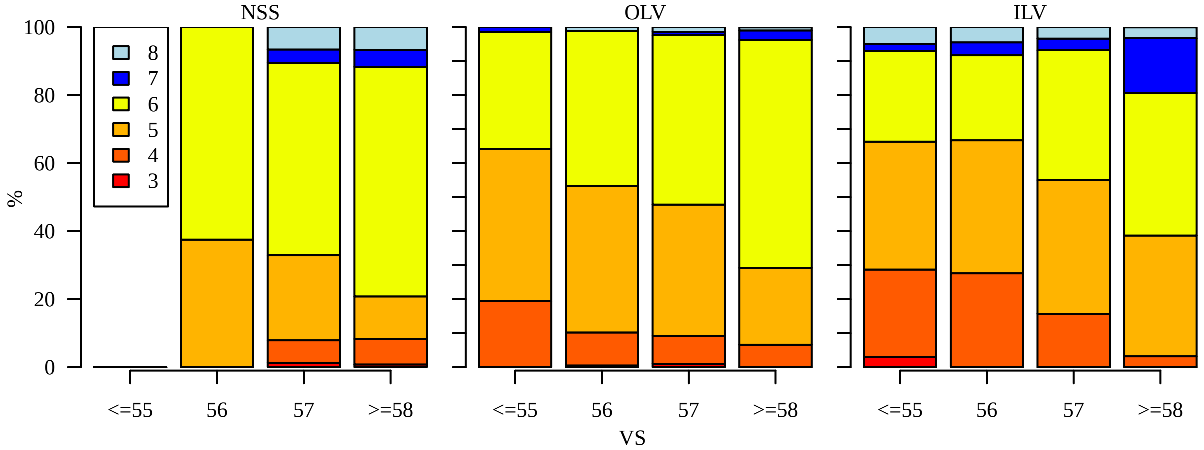

Figure 26: Stage of maturity composition for vertebral groups for herring typed as NSS, OLV and ILV in the spawning season 2012.

To look at potential differences in investment in gonads, the gonadosomatic index (GSI) and gonad condition (gonadK) of different groups were compared (Figure 27). The differences of GSI and gonadK along the three groups were significant (ANOVA; p<0.001), but the Tukey range test showed only significant differences between NSS compared with OLV and ILV. Comparing individual groups demonstrated significant differences between NSS versus both OLV and ILV, where the values within maturity stages for both GSI and gonadK were lower in NSS herring (ANOVA; p<0.001), indicating a lower investment into gonad production.

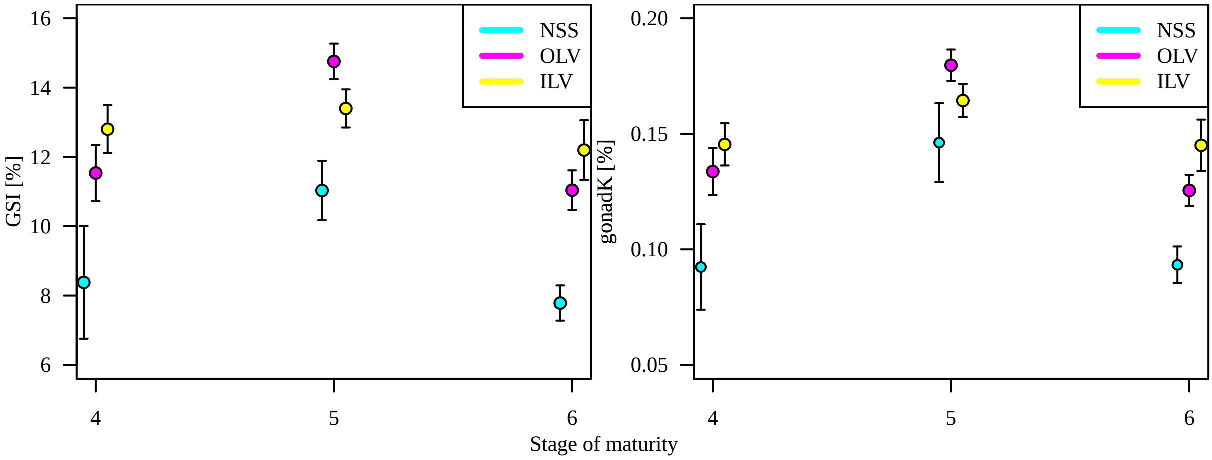

Figure 27: Comparison of gonadosomatic indix and gonad condition in relation to stages of maturity between herring typed as NSS, OLV and ILV in the spawning season 2012.

3.3 Scale 3: Analyses of telemetry data during the 2012 spawning season in Landvikvannet and connected fjords

A total of 61 herring were tagged in 3 tagging experiments showing total body lengths ranging from 19.0–35.0 cm with a mean value of 27.38 cm and ages ranging from 2–15 years with a mean value of 4.41 years (Figure 28).

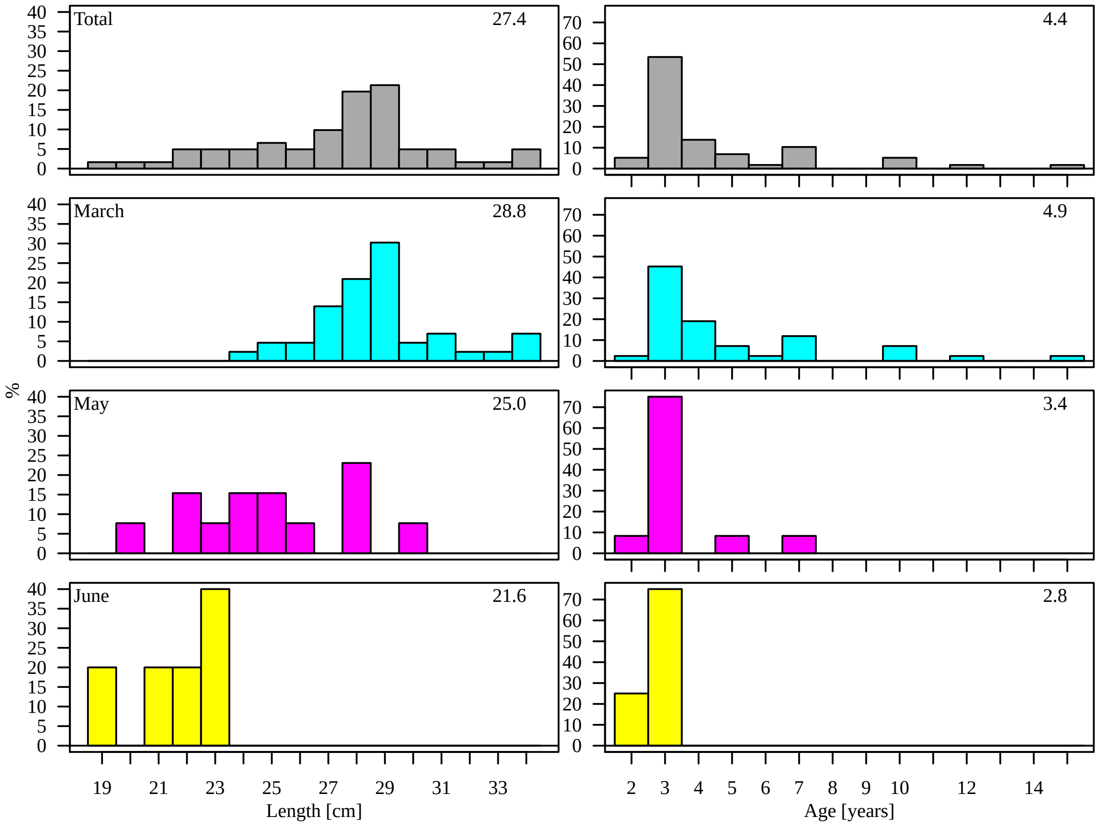

Figure 28: Length and age distribution of tagged herring from Strandfjorden including the mean, separated into the different tagging experiments.

More than 50% of the tagged herring were at the age of 3 years. It was not possible to identify NSS along the tagged herring since no otoliths could be removed. Both length and age (Kruskal-Wallis; $p<0.001$) was found to differ between the tagging experiments. Pair wise comparisons between the different experiments were also significant for age and length (Mann-Whitney; $p<0.001$), with the exception of the experiment in May versus June for age. The main tendency was a significant decrease in body length and age from the experiment in March, May to June.

After tagging and releasing most herring left Strandfjorden within 24 hours and stayed in Bufjorden before they showed many different behavioral movements. While some left the study region immediately, others stayed within the coastal area or even entered the lake (Figure 29). During the monitoring period, from March until October, 16 herring apparently died within the study area (inferred from ceasing of signals or movement), including all tagged herring in June. These fish were excluded from the following analyses, except 3 individuals (ID: 6, 35, 53) which survived more than 3 days staying inside the study system and were therefore included until they all died in Strandfjorden. All other herring died within 3 days, most of them did not even reach Bufjorden. For the surviving herring four typical behavioral patterns could be identified: a) migration back and forth between Strandfjorden and Bufjorden, b) similar migration as in a) but including visits in Landvikvannet, c) leaving the study area directly to the open sea without staying in Bufjorden longer than a week and d) leaving the study area to the open sea after staying in Bufjorden for a longer time. For herring tagged in March the most common behavioral pattern was a) followed by d), c) and b) (Figure 30 and Table 9). Among tagged herring in May all patterns occurred with similar frequency. But still the distribution of different behavioral patterns along the different experiments was not significantly influenced (Fisher's Test; $p>0.05$). Neither age nor total length (Table 9) differed significantly for the different behavioral patterns within an experiment (ANOVA; $p>0.05$), except the total length in March (ANOVA; $p<0.05$) where individuals migrated between Bufjorden and Strandfjorden were larger than other herring. Also pairwise comparisons of age and length did not demonstrate

Table 9: Comparison of the four behavioral patterns along the tagging experiments, a) migration between Strandfjorden and Bufjorden, b) migration into Landvikvannet, c) leaving the system within a week, d) staying in Bufjorden for more than a week.

	Behavioral pattern			
	a)	b)	c)	d)
Composition				
March	37.5%	7.5%	25.0%	30.0%
May	25.0%	25.0%	25.0%	25.0%
Mean age [years]				
March	5.5	5.7	4.1	5.0
May	2.5	4.0	5.0	3.0
Mean length [cm]				
March	30.3	28.0	26.7	27.9
May	25.0	28.0	25.0	26.5

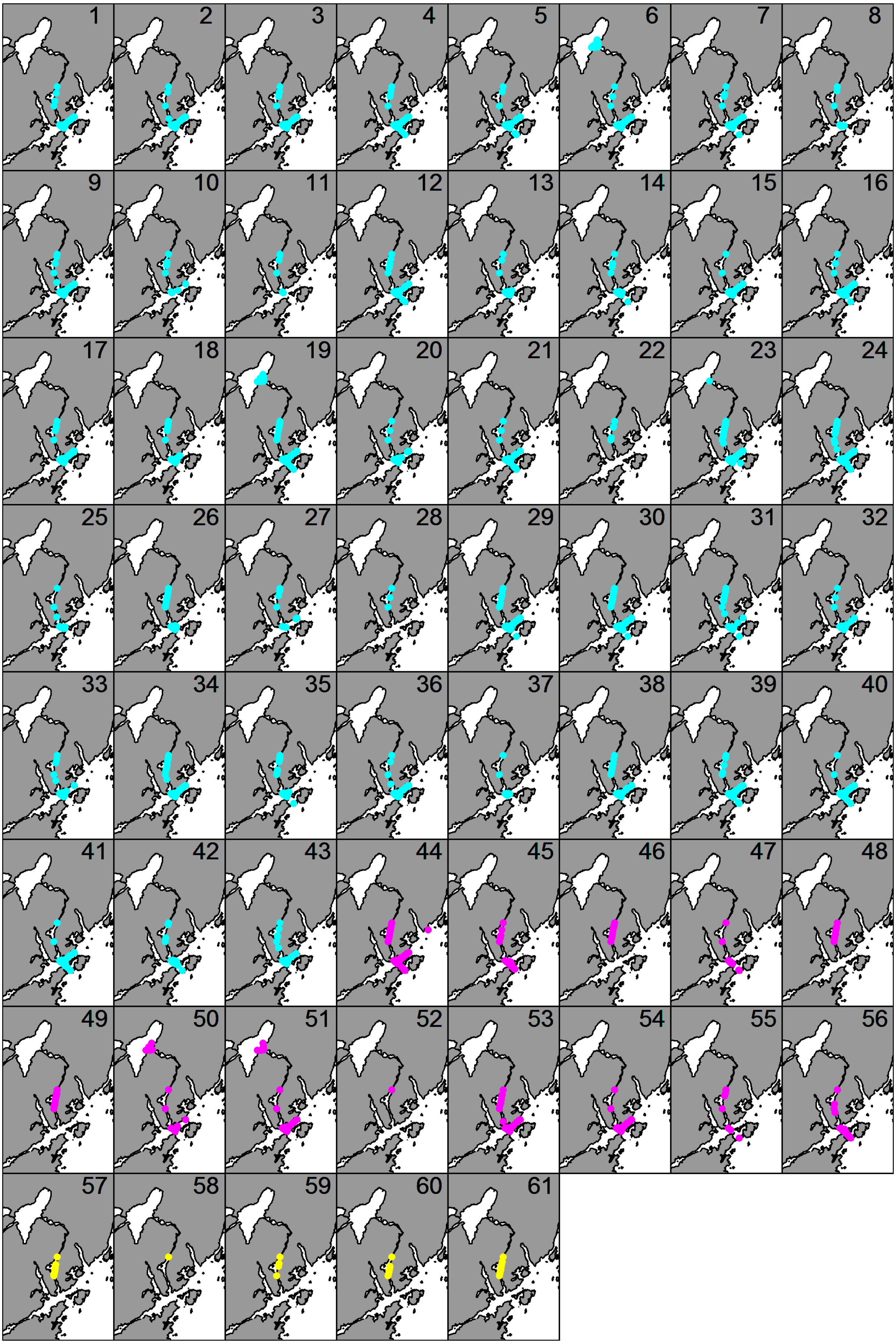

Figure 29: Positions of individual Atlantic herring during spawning season 2012 estimated from acoustic monitoring including the Fish ID. Separated into the different tagging experiments: Cyan = March, Purple = May, Yellow = June. For map scale and details, see Figure 2.

significant differences for the experiment in March versus May for each behavioral pattern, except the lower age of herring in May showing behavioral pattern a) (T-test; p<0.05).

Behavioral pattern b) could be seen for 5 herring (ID: 6, 19, 23, 50, 51; age: 10, 4, 3, 3, 5) which entered Landvikvannet at least once during the monitoring period. Three of the 5 herring entering the lake were tagged during the experiment in March. All migrations, defining behavioral pattern a), between Bufjorden and Strandfjorden took place within 18 days after tagging, except two. Even all migrations were within a small time interval none of the herring migrated at the same time or in the same group. The migration between Bufjorden and Strandfjorden (mean duration: 1.7 hours) was significantly longer (T-test; p<0.05) than the reciprocal one (mean duration: 0.9 hours). Still the fastest migration was recognized on the way back into Strandfjorden, it last only 12 minutes, while the longest migration last more than 7 hours on the same way. The

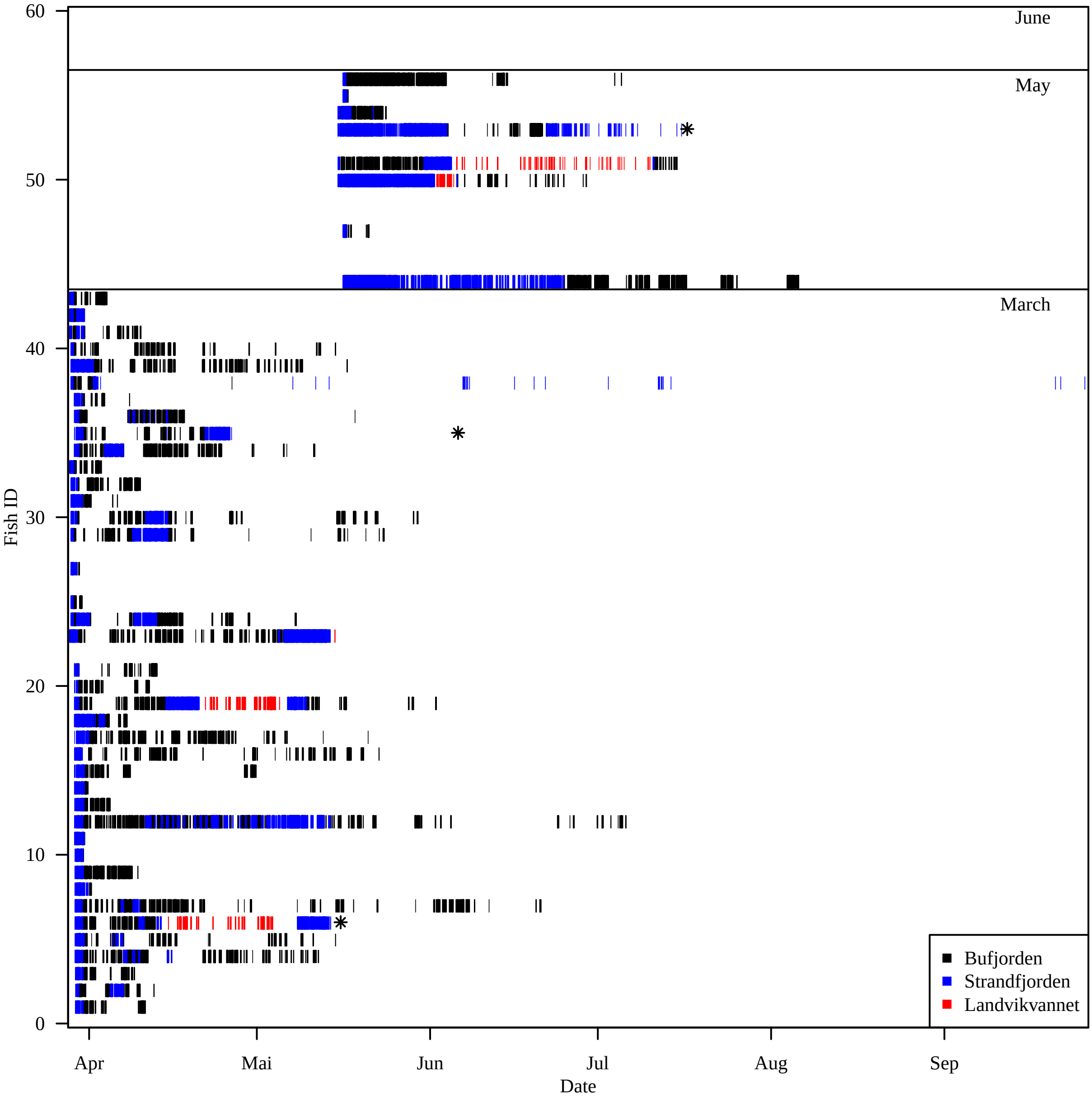

Figure 30: Different position within the monitoring system of individual herring, * day of death , herring showing a behavior which defined them as dead within 3 days after tagging were excluded.

migration was significantly influenced by the time of day (Chi²; $p<0.001$) but not by the tides (Chi²; $p>0.05$). Herring migrated during the day and mostly in the evening from Bufjorden into Strandfjorden. The migration for the reciprocal way was during the evening and mostly in the night. No herring migrated in the morning. Similar results were found for migrations into Landvikvannet. Due to the low number of individuals migrating into the lake and the big range for the duration there was no significant differences (T-test; $p>0.05$) between the mean migratory duration for the way from Landvikvannet into Strandfjorden (22.3 hours) and the reciprocal way (41.9 hours). The fastest herring on the way into the lake (10.0 hours) was also the fastest one on the way back (12.7 hours). Neither the tides nor the time of day (Chi²; $p>0.05$) had a significant influence on the migration between Strandfjorden and Landvikvannet, even 3 out of 5 herring migrated during the evening into the lake or during the night backwards. Only two herring were detected in Landvikvannet at the same time.

All herring entering Landvikvannet left Strandfjorden within 24 hours to stay in Bufjorden, except one individual (ID: 50). This herring stayed for more than 2 weeks in Strandfjorden before it entered the lake. Also the other herring stayed at least 2 weeks in the connected fjords before they entered Landvikvannet. On the way from Bufjorden to Landvikvannet herring swam between 5 and 9 days in Strandfjorden, two individuals (ID: 6, 23) also showed reciprocal migrations between Strand- and Bufjorden before swimming into Landvikvannet. The herring which stayed in Strandfjorden (ID: 50) spent 4 days in Landvikvannet before it migrated directly into Bufjorden within 24 hours where it stayed for 23 more days. One individual (ID: 23) was only recognized for one hour in Landvikvannet, and this was the last recognized signal by any receiver. Therefore it may be possible that this herring is still inside Landvikvannet. The 3 other herring spent 16, 25 and 36 days in Landvikvannet (ID: 6, 19, 51). Those 3 herring were recognized by all receiver units inside the lake, but it was not possible to detect in which direction they entered the lake. Additionally some time intervals without any signal were detected for those 3 individuals, indicating that these herring not only stayed at the beginning of Landvikvannet. There were no significant differences between herring tagged in March or in May, neither for age, length or duration inside the lake (ANOVA; $p>0.05$). None of the herring left the study system immediately after leaving the lake; they stayed at least 4 days in Bufjorden and Strandfjorden.

All herring staying for more than 3 days in the study system spent more than 50% of the time in Bufjorden (Figure 31), except three herring which entered Landvikvannet (ID: 6, 19, 51) and two herring which died in Strandfjorden (ID: 6, 53). Those herring spent more than 50% or 25% in the lake. Herring leaving the study system within 3 days or less passed through Bufjorden within a few hours.

Beside the migratory patterns some similarities could be defined due to the duration of individual herring within the monitoring region. The minimum duration was less than 24 hours while the maximum duration was 182 days (Figure 32), leading to 4 different groups (Appendix Figure A.7). The first two groups were defined as very fast and fast herring, which left the area within the first 10 days (40.8%) or more than 10 days and up to 20 days (20.4%). Between these two

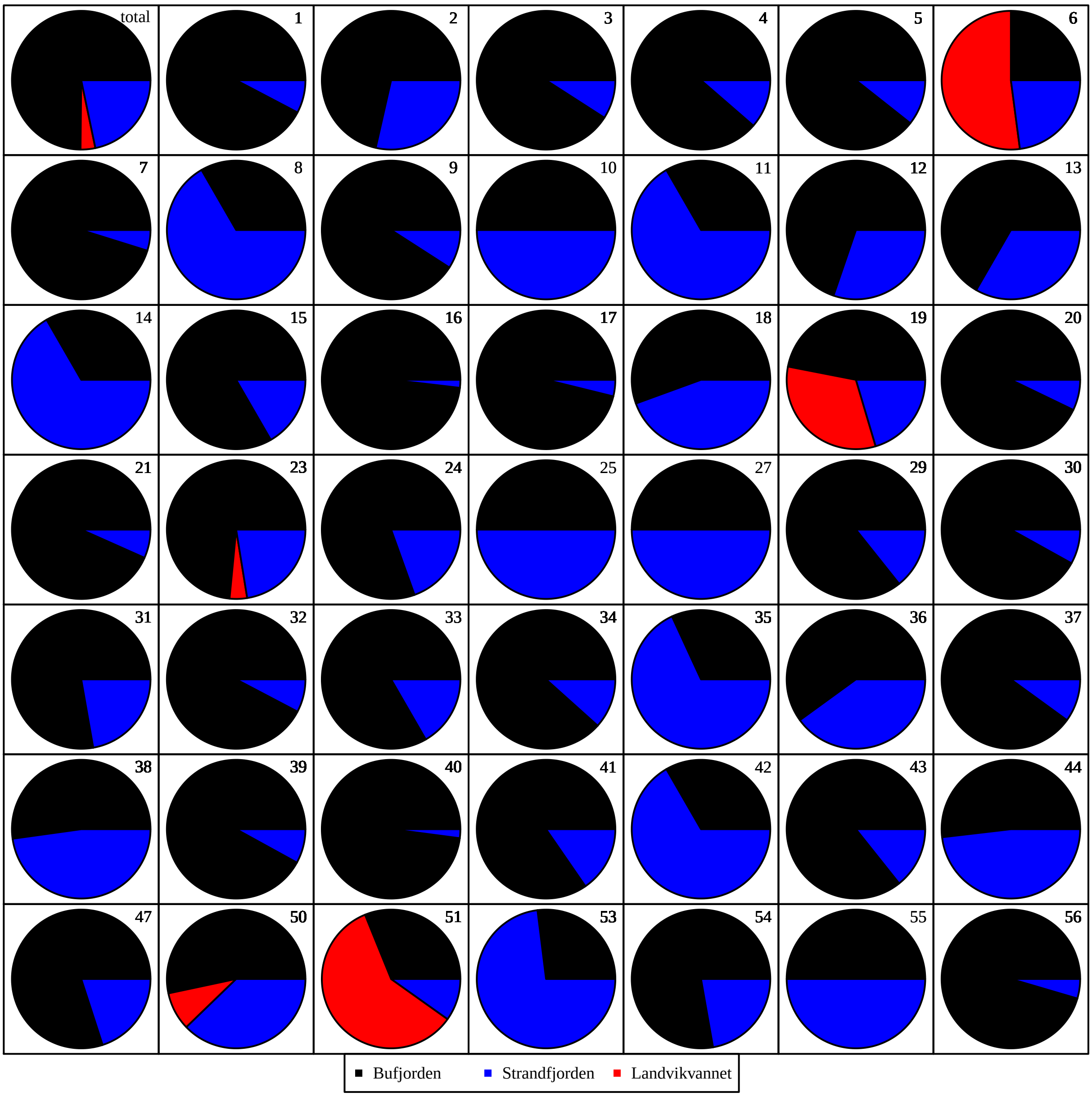

Figure 31: Days of duration at the different positions within the study system for pooled data of tagged herring and each individual herring, herring showing a behavior which defined them as dead within 3 days after tagging were excluded.

groups and the third a large gap exist where no herring has left the area. The moderate herring defining the third group left the area between 40 and 62 days (30.6%). The slow herring and last group stayed longer than 62 days in our monitoring system before they left to the open sea (8.2%). Neither total length of the herring nor the age (ANOVA; $p>0.05$) differed significantly within the four groups. Comparing the four behavioral patterns with the duration time of individual herring inside the monitoring system showed significant differences of the four groups (Fisher's test; $p<0.001$). While 75.0% of the slow herring and 52.9% of the moderate herring migrated forth and back between Bufjorden and Strandfjorden, only 30.0% of the fast and 17.6% of the very fast individuals migrated inside the system. Along the herring without any migration only 11.8% of the very fast herring, 25.0% of the slow and 28.6% of the moderate herring stayed in Bufjorden, while 70.0% of the fast herring showed this behavioral

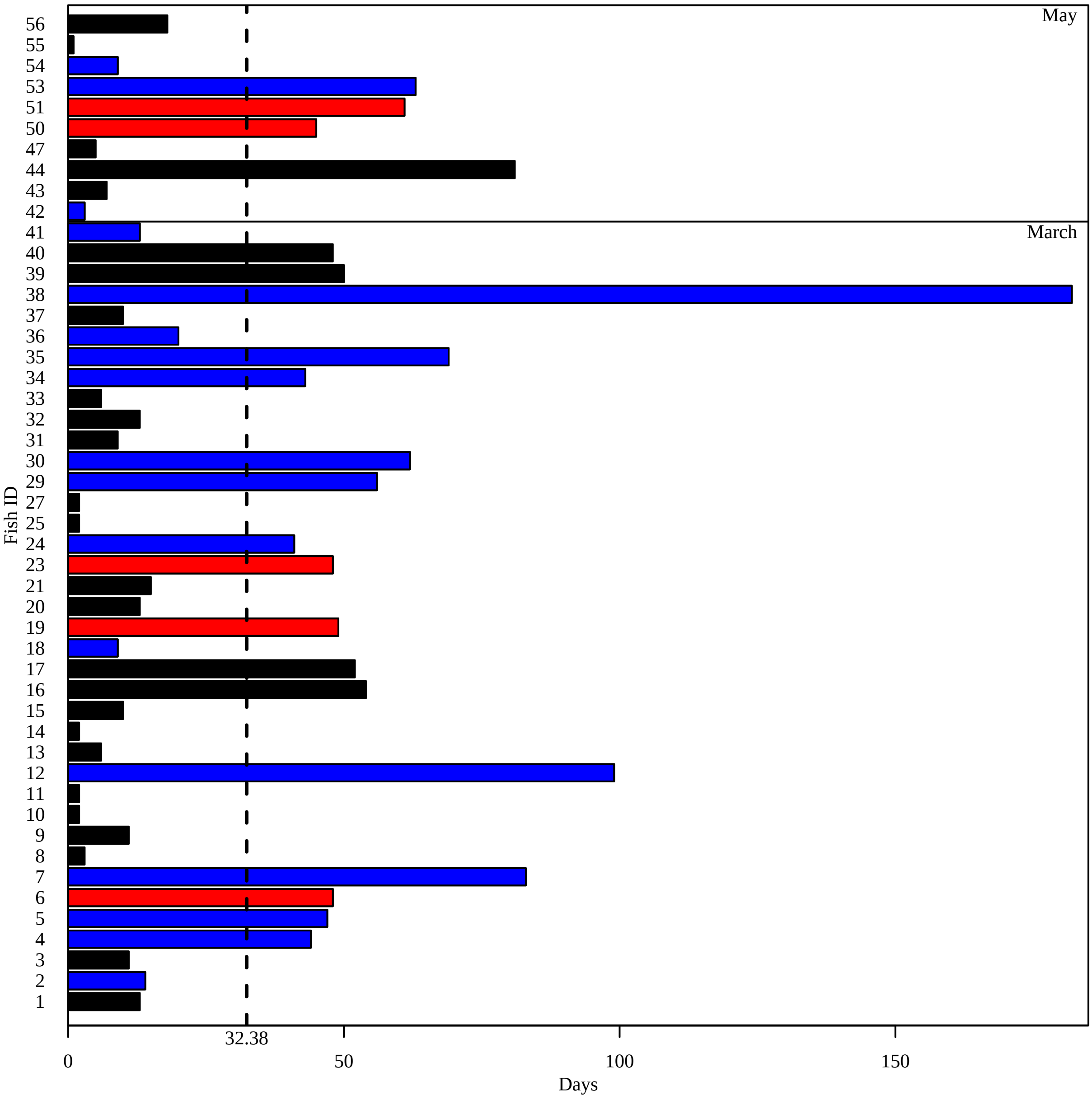

Figure 32: Duration of tagged herring within the telemetry system, dashed line shows the mean duration of all tagged fish, blue bars indicate migration patterns, red bars Landvikvannet, black bars no migartion, herring showing a behavior which defined them as dead within 3 days after tagging were excluded.

pattern. All herring entering the lake left the system after a moderate time and due to the definition of the behavioral patterns and the duration groups, all herring leaving the system directly were very fast. The duration time did not differ significantly between the two tagging experiments in March and May (Kruskal-Wallis; $p>0.05$).

In addition to the stay duration there were significant differences for the time of leaving the system. The 24 hours of a day were separated in 4 groups; night from 0:00–6:00, morning from 6:00–12:00, day from 12:00–18:00 and evening from 18:00–24:00 (Figure 33). More than half of the tagged herring left the system during the night (53.1%), while 26.5% left during the evening, only 6.1% and 14.3% during day and morning, respectively. There were no significant differences for length or age (ANOVA; $p>0.05$) and no significant influence of low or high tide (Chi²; $p>0.05$) on the herring for leaving the system (Table 10). The tagged herring left

Table 10: Contingency table demonstrates the time of day for leaving the monitoring system concerning the tide of tagged herring.

Tide	Night	Morning	Day	Evening
High	10	1	1	6
Low	15	6	2	7

the system without any clear pattern; both exits were used by approximately the same amount of herring (southwards 38.8%; eastwards 44.9%) (Appendix Figure A.8). There was no significant influence on the leaving station through the different behavioral patterns. The leaving station was not influenced significantly by age or length for herring tagged in the different experiments (ANOVA; p>0.05). For 12.2% the last detection was at station 5 which may be an indication for the migration into the inner Bufjorden. But we cannot be sure that those herring have left the area or not, for example when they left the area within the signal interval of the transmitter before a new signal has been transmitted. Neither leaving time nor station were significantly influenced be the tagging experiment (Kruskal-Wallis; p>0.05).

According to the results for the detailed spawning season in 2012 showing that most of 3 year old herring could be identified as NSS it was not possible to identify the 3 year old tagged herring as NSS or at least one group of its own. Neither duration nor behavioral patterns were influenced significantly by age. For the behavioral pattern a), c) and d) and for the four duration groups most herring were 3 years old. According to the age distribution of NSS in 2012 no herring were 2 years old and younger or 8 years old and older and were therefore compared separately to identify differences along the tagged herring. But even comparing those herring demonstrated

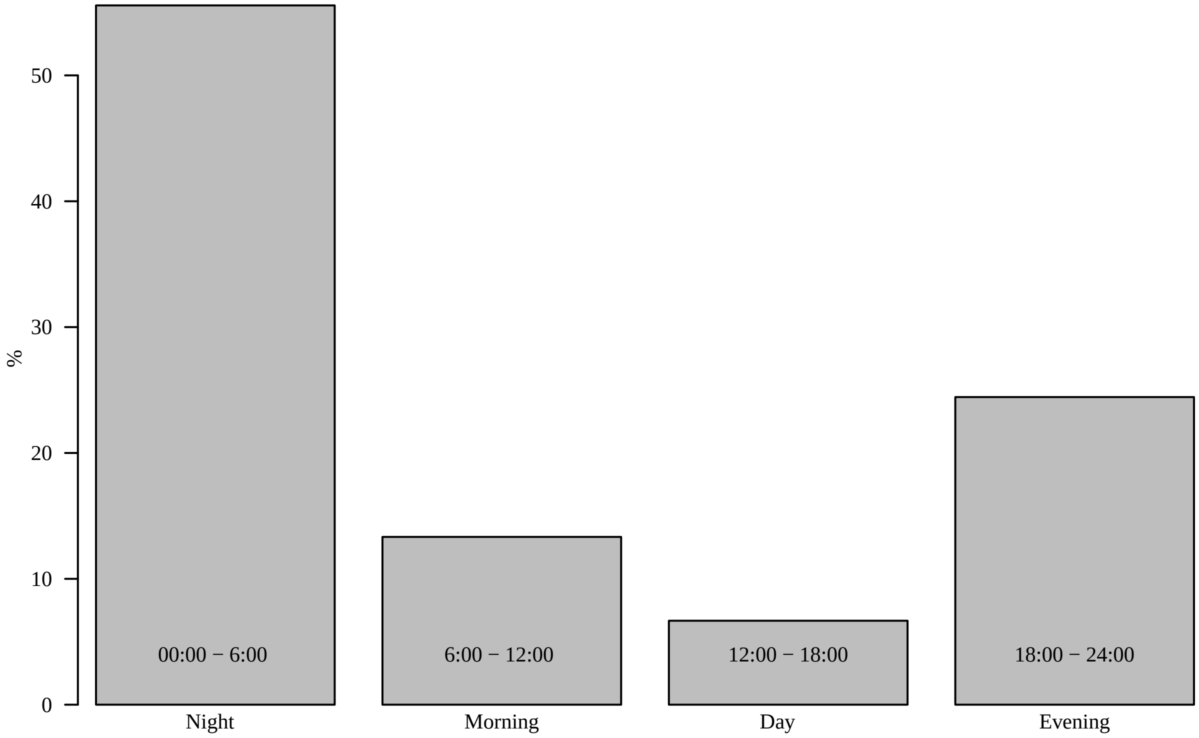

Figure 33: Time of day when tagged herring left the study area, where the night was set from 0:00 until 6:00, morning from 6:00 until 12:00, day from 12:00 until 18:00 and the evening from 18:00 until 24:00, herring showing a behavior which defined them as dead were excluded.

no significant differences in behavioral patterns, duration and leaving time and station. Also comparing 3 year old herring exclusively with all other ages did not differ significantly. As the results of 2012 demonstrated significant differences in growth between NSS and OLV, 3 year old tagged herring were compared due to their total length. Concerning the length distribution of 3 year old herring (Appendix Figure A.9), they were separated in herring at lengths >=27 cm and bigger. Still there were no significant differences in behavioral patterns, duration and leaving time and station along the two length groups. Also separating herring in other length groups did not indicate any significant differences. There were also no significant differences between herring tagged during the different tagging experiments in the season, neither for age nor for length groups. Therefore it was not possible to identify any special behavior for a single group, apparently not as NSS.

Additionally to the monitoring system in our study area another monitoring system, Sømskilen, exist approximately 20 km northwards near the town of Arendal and the Flødevigen marine research station, where 40 receiver units were moored to investigate the behavior of cod. The receiver units are identically with the ones we used in our study area. This system was not included in the methods chapter as it was not part of the planned study of the Master thesis. Still, it turned out that some tagged herring also were recorded here and these were included in the results as a demonstration of potential migrations outside the monitoring system in Landvik, Strandfjorden and Bufjorden. Three of the tagged herring (ID: 19, 34, 44; age: 4, 5, 3) were detected in Sømskilen and showed different behavioral patterns (Figure 34). One individual (ID: 19) also migrated back and forth between the two monitoring systems and stayed for a longer time in the Sømskilen area. All northwards migrating herring left the monitoring system through the eastern entrance during the night. Herring needed between 2.1 and 33.5 days with a mean travel time of 12.1 days. Excluding the travel time of 33.5 days of one herring, the mean

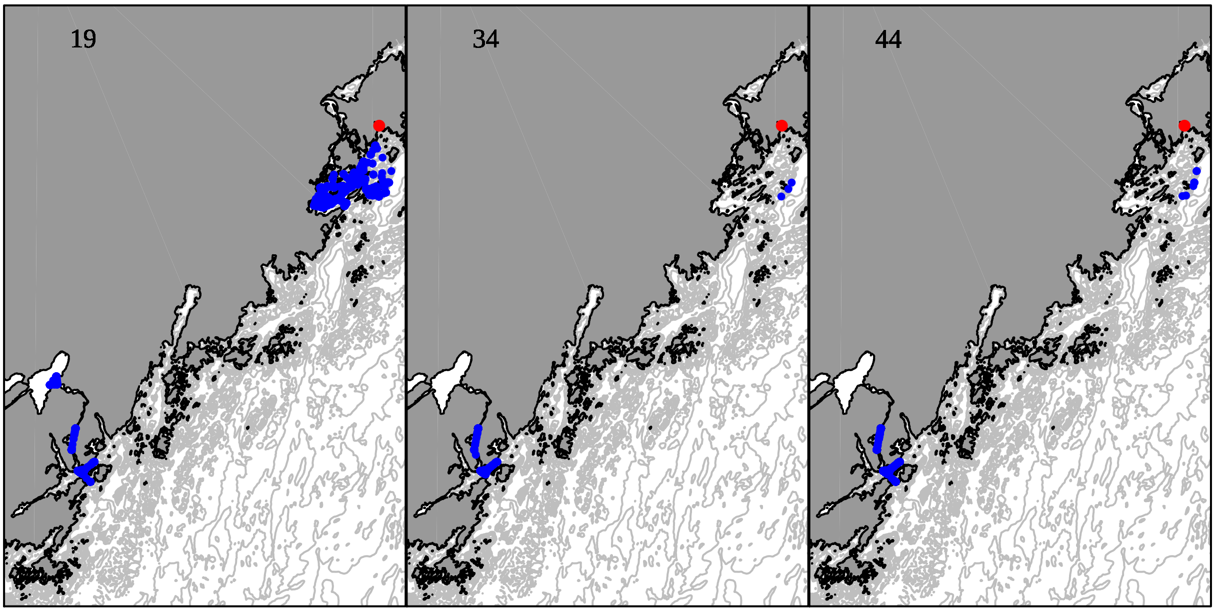

Figure 34: Positions of individual Atlantic herring during spawning season 2012 estimated from two acoustic monitoring systems including the Fish ID (South: study area; North: Sømskilen area; red point = Flødevigen marine research station).

travel time was 5 days which is more precise because the travel duration for the other three migrations was maximum 6.5 days. According to the air-line distance of 16.6 km between station 4 in the study system and the first station in Sømskilen, herring had an average travel speed of 138.4 meter per hour. Herring reached the second area all over the day, except in the morning and stayed between 1 hour and more than 96 days, while the herring staying more than 96 days had not left the system at the day of downloading (10/09/2012). All herring left the system in the Northeast all over the day without any clear time pattern. The herring were just recognized at the outer most receiver stations, except one herring (ID: 19). This particular herring was recognized twice at both systems and also entered Landvikvannet before it left the study system on its way to Sømskilen. The first time it stayed for 1.3 days in the Sømskilen area before it migrated back to the study area which last only 3.3 days. In the study area the herring was just recognized be the southern receiver (1 Pølseskjær) for the next 5 days, before it migrated back to the Sømskilen area swimming inside the system until the day of downloading.

3.4 Analyses of environmental data and potential effects on results from herring analyses at scales 1–3

Historical environmental data of the coastal areas were analyzed and compared to demonstrate their effects on results from herring analyses at scales 1–3. For comparison, the variations of mean temperature and salinity during the spawning season from March until June were analyzed. At scale 1 environmental data of 5 stations along the west coast demonstrated the same fluctuations and were peaking at the same time (Figure 35). All together the temperature indicates an increasing tendency. The more northern location of the station the less were the fluctuations and the mean temperature. The temperature was peaking in the spawning seasons 1974, 1983, 1989, 1998–1999 and 2007. Those peaks can be traced along all stations, except the peak in 1983 in Lista. The temperature peaks of the west coast were comparable with the peaks in Flødevigen at the east coast of Norway. Also the variation of the salinity was similar along the west coast. In 1987 the salinity was at a minimum at 20 m depth, otherwise it fluctuated around the mean. Neither the variation of temperature nor salinity can be compared with the variation for VS, length and age along the different years, or year classes for WC herring.

Also data from Flødevigen at the east coast of Norway were analyzed which were comparable to the temperature peaks demonstrated along the west coast stations (Figure 36). The variation could be traced for all depths for temperature as well as salinity. The overall mean surface temperature was around 9 °C with increasing tendency. There were three extremely cold periods in 1977–1979, 1986 and 1994. Also there was a temperature peak for the spawning season in 1973, 1982 and 1988. Otherwise the variation tended more to be warmer than the mean. The fluctuations of the salinity in the upper two meters were extremely high compared to the deeper measurements. There were not as many big changes as for the temperature and no years with extreme changes in salinity were detectable, except 1998–2000. As well as for the data from the west coast, there

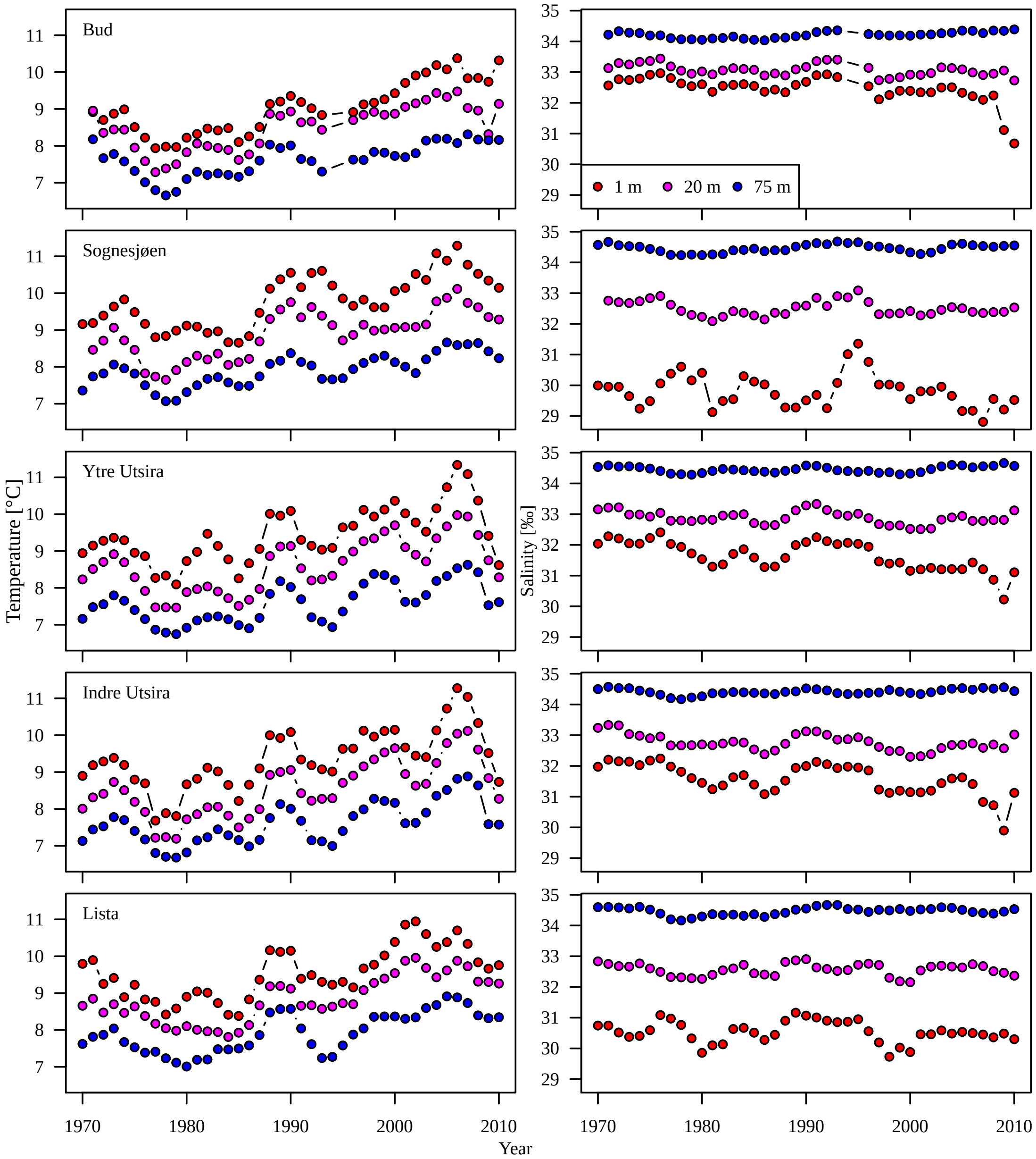

Figure 35: Inter-annual variations in temperature and salinity at 5 monitoring stations along the west coast of Norway during the spawning season since 1970 for different depths. Values given are 3-year running means.

was no visible pattern for the variation of temperature and salinity compared to the variation of VS, length or age for the corresponding years or year classes of EC and LV herring.

Even historical environmental data of Landvikvannet were compared (Figure 37). Therefore the variations of the mean temperature and salinity in May were compared for different depths, also to show the influence on VS and growth. The variation of temperature and salinity since 1983 was the same for all depths, except 2000 for the temperature which decreased in depths of 5 m and 10 m, but increased at the surface compared to the previous and following year. All in all there was no clear trend for the temperature or a specific year with high or low mean temperature in May. For the salinity the main tendency is decreasing since 1983. In 1995 the salinity was extremely low compared to the other years. However, there was found no relation to the fluctuation on herring analyses.

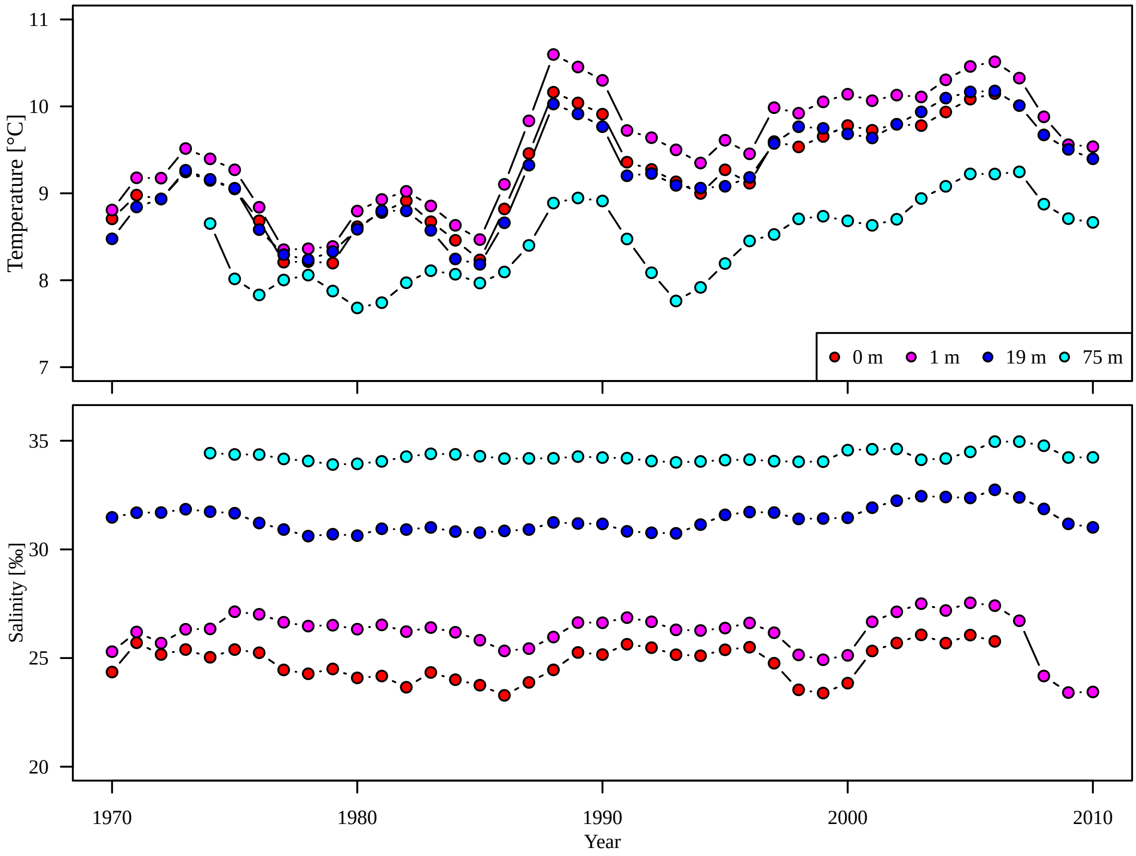

Figure 36: Inter-annual variations in temperature and salinity in Flødevigen during the spawning season since 1970 for different depths. Values given are 3-year running means.

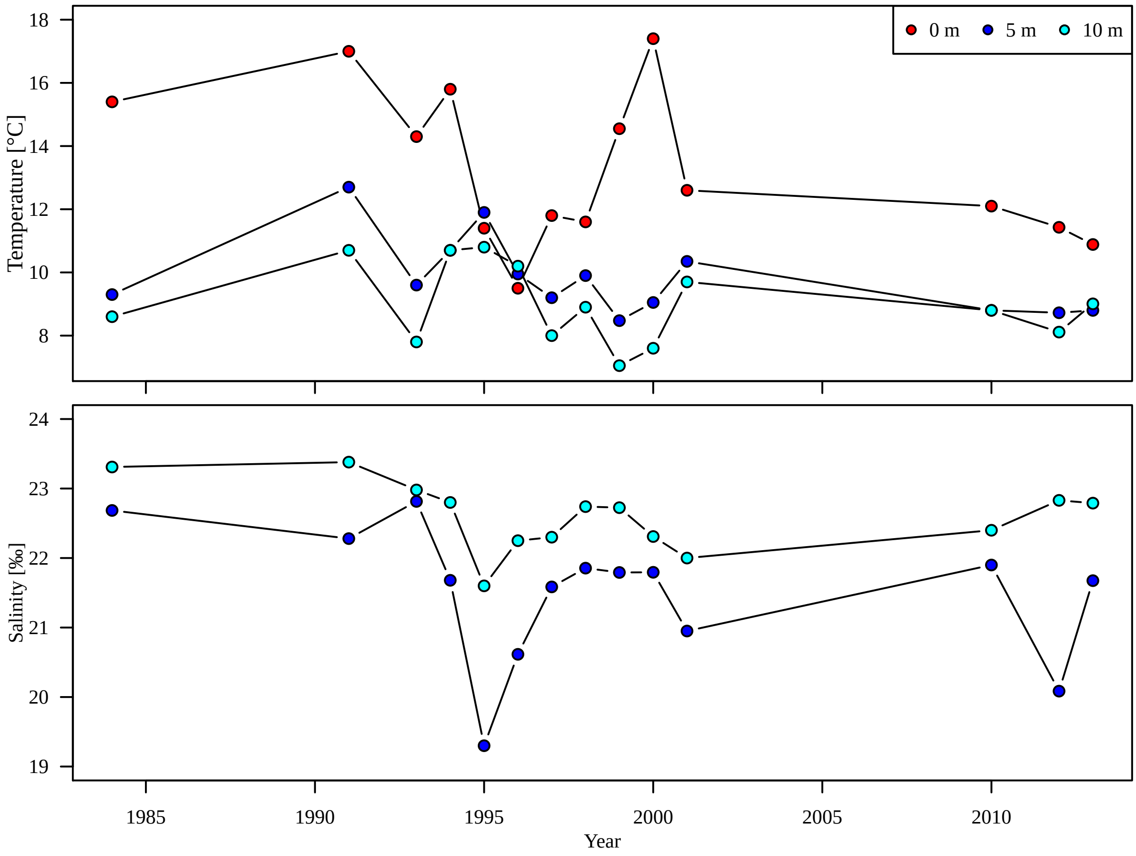

Figure 37: Inter-annual variations in temperature and salinity in Landvikvannet during May since 1984 for different depths.

At scale 2, during the spawning season 2012, an extensive time serie of environmental data was collected in Landvikvannet and the inner part of Strandfjorden. Therefore the temperature, salinity and oxygen/hydrogensulfide concentration through the whole water column were measured when biological samples were taken to investigate biological changes in connection with environmental changes. The results of environmental data taken in Landvikvannet changed for all measured abiotic factors within the sampling period (Figure 38). The surface temperature increased from less than 2 °C in the beginning of March to more than 20 °C in August. Deeper than 7 m the temperature stayed constant around 7–8 °C for all samples. Also the depth where the temperature stayed constant increased during the year. The surface salinity also increased during the year from 2‰ up to 7‰. The increase of salinity with depth was much stronger than for the temperature. Therefore the salinity was above 20‰ for all samples at a depth of 4 m, the constant salinity of 23‰ was reached at 6 m, except for the sample taken in May. The O_2/H_2S concentration varied as well during the sampling period. While the oxygen concentration in June and August was lowest at the surface it increased down to a depth of 5 m, after which it decreased rapidly within one meter to almost 0 ml/l. The O_2 concentration taken in May or before was higher at the surface but decreased faster and was depleted higher in the water column (Figure 39). The largest depth where oxygen was depleted was 3.5 m in the beginning of March and the lowest depth was 5.5 m in June. When the oxygen was depleted the concentration of hydrogensulfide increased. The H_2S concentration was highest for all samples at a depth of 10 m. Also the concentration at the bottom increased from the samples taken in March until August.

The abiotic factors also varied during the year in the inner part of Strandfjorden but differently

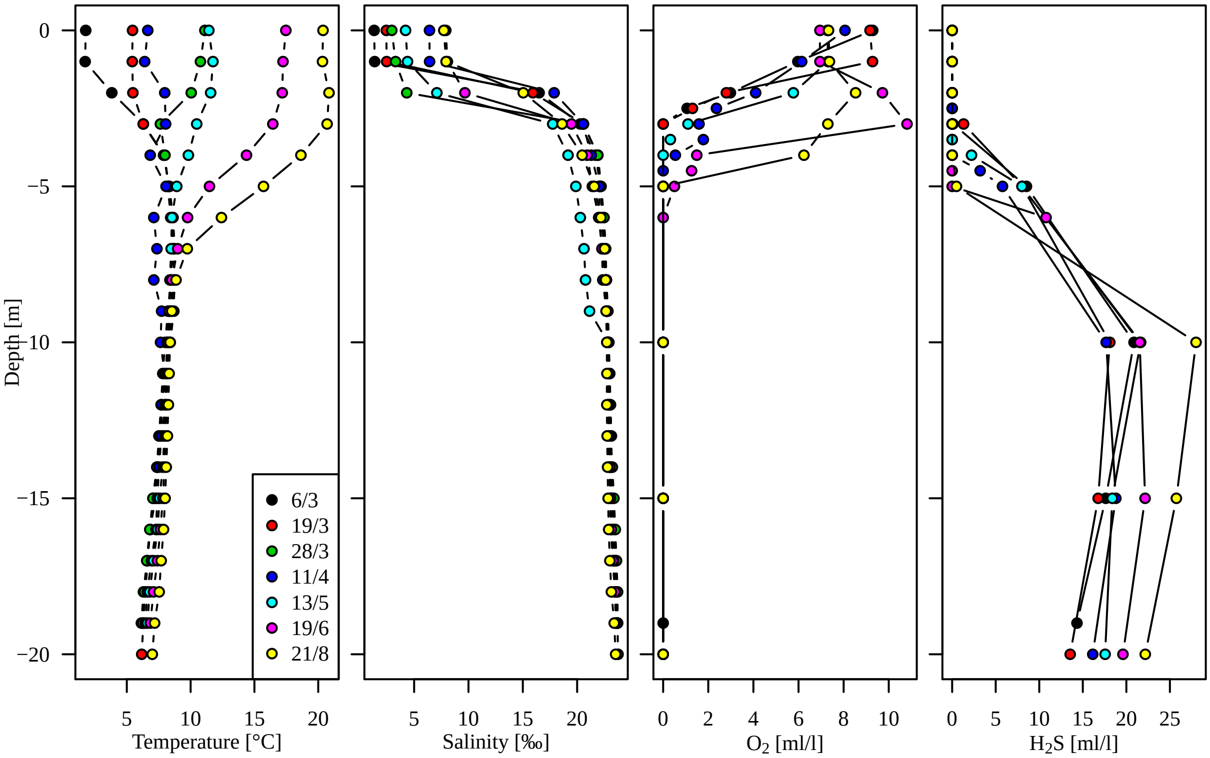

Figure 38: Temperature, salinity, oxygen and hydrogensulfide concentration by depths for each sampling date taken in Landvikvannet during the season in 2012.

than in Landvikvannet (Figure 40). The surface temperature increased from the beginning of March until August, but in contrast to Landvikvannet also the bottom temperature increased from 6 °C to 14 °C. For the salinity no clear pattern was visible along the surface, it varied for all the samples. The constant salinity of approximately 33‰ was reached in a depth of 6 m. All in all the salinity in the inner part of Strandfjorden was always higher than compared for Landvikvannet. The O_2 concentration along the surface decreased during the sampling period. While it decreased only by about 2 ml/l from the surface to the bottom for samples taken in June or earlier, it decreased by 5 ml/l in August to less than 1 ml/l. But still there was no H_2S found in the inner part of Strandfjorden for all samples.

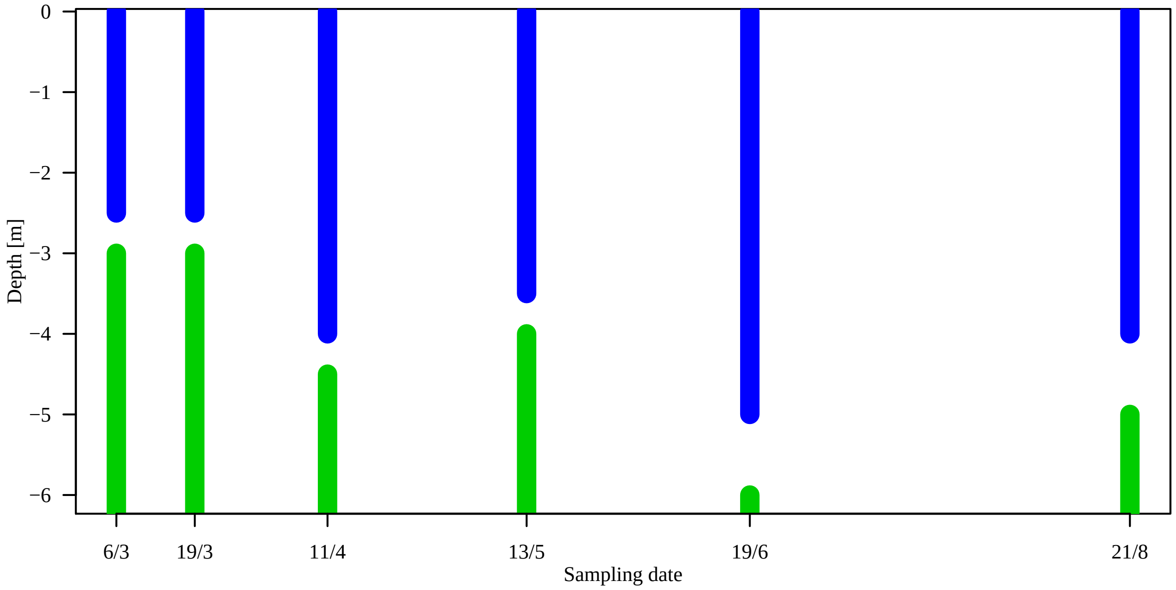

Figure 39: Depth of oxygen layer by sampling date in Landvikvannet taken in 2012 (blue = existence of oxygen, green = depleted oxygen, existence of hydrogensulfide).

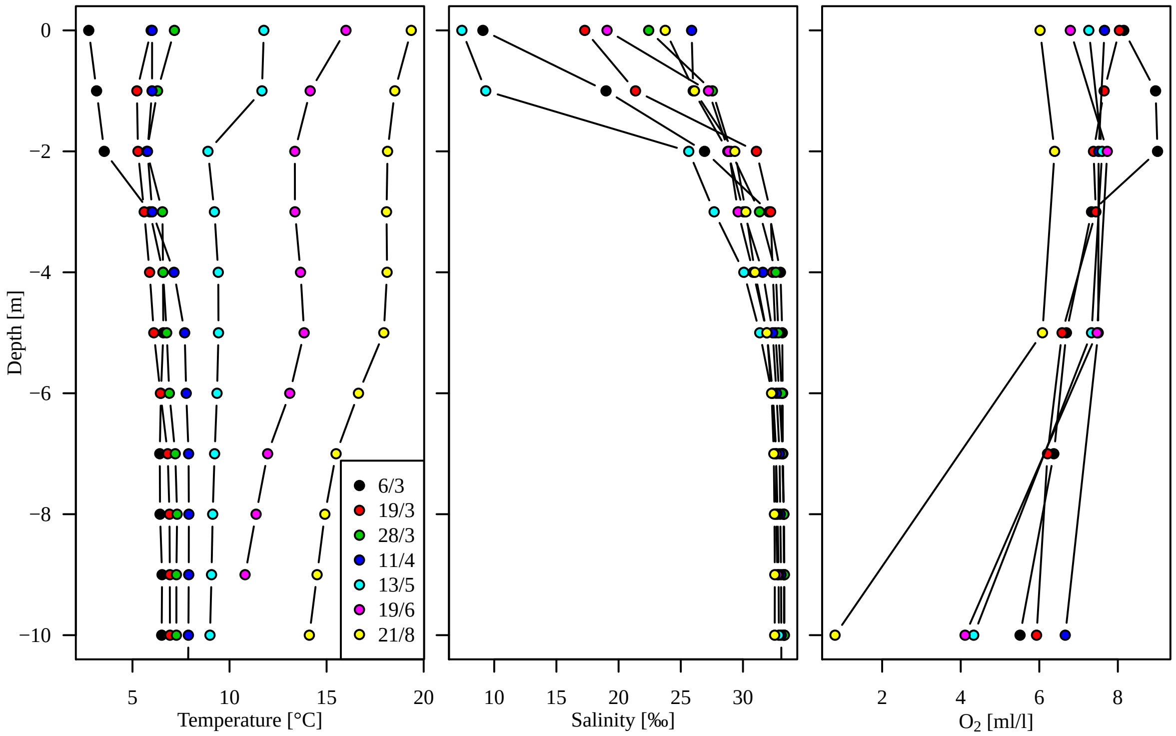

Figure 40: Temperature, salinity, oxygen and hydrogensulfide concentration by depths for each sampling date taken in Strandfjorden during the season in 2012.

At scale 1, testing the mean temperature and salinity against VS and growth of LV and EC herring did not correlate significantly for Landvikvannet and Flødevigen (Pearson; p>0.05). Also VS and growth of WC herring were compared and demonstrated no significant correlation, neither for temperature nor for salinity along all environmental stations of the west coast (Pearson; p>0.05) (Appendix Figure A.10–Appendix Figure A.15).

At scale 2, the same comparison of the mean temperature and VS indicated a significant decrease of VS with increasing temperature for both OLV and ILV (Regression; p<0.05) (Figure 41). VS of OLV were compared with environmental data of Strandfjorden at a depth of 5 m, and ILV with data from Landvikvannet at a depth of 3 m. The depths of 5 m, respectively 3 m, were selected according to observed herring schools by echo sounder. For ILV the sample from August was excluded because no spawning occurred. The testing of different depth (0 m, 10 m and 20 m) did not show any significant correlation, except the data at 20 m depth in Landvikvannet. This was also excluded because of the anoxic layer. There was no correlation between VS of OLV and ILV versus salinity for any depths in Strandfjorden and Landvikvannet. For NSS no significant correlation could be demonstrated at all, neither for temperature nor salinity in both ecosystems, Strandfjorden and Landvikvannet.

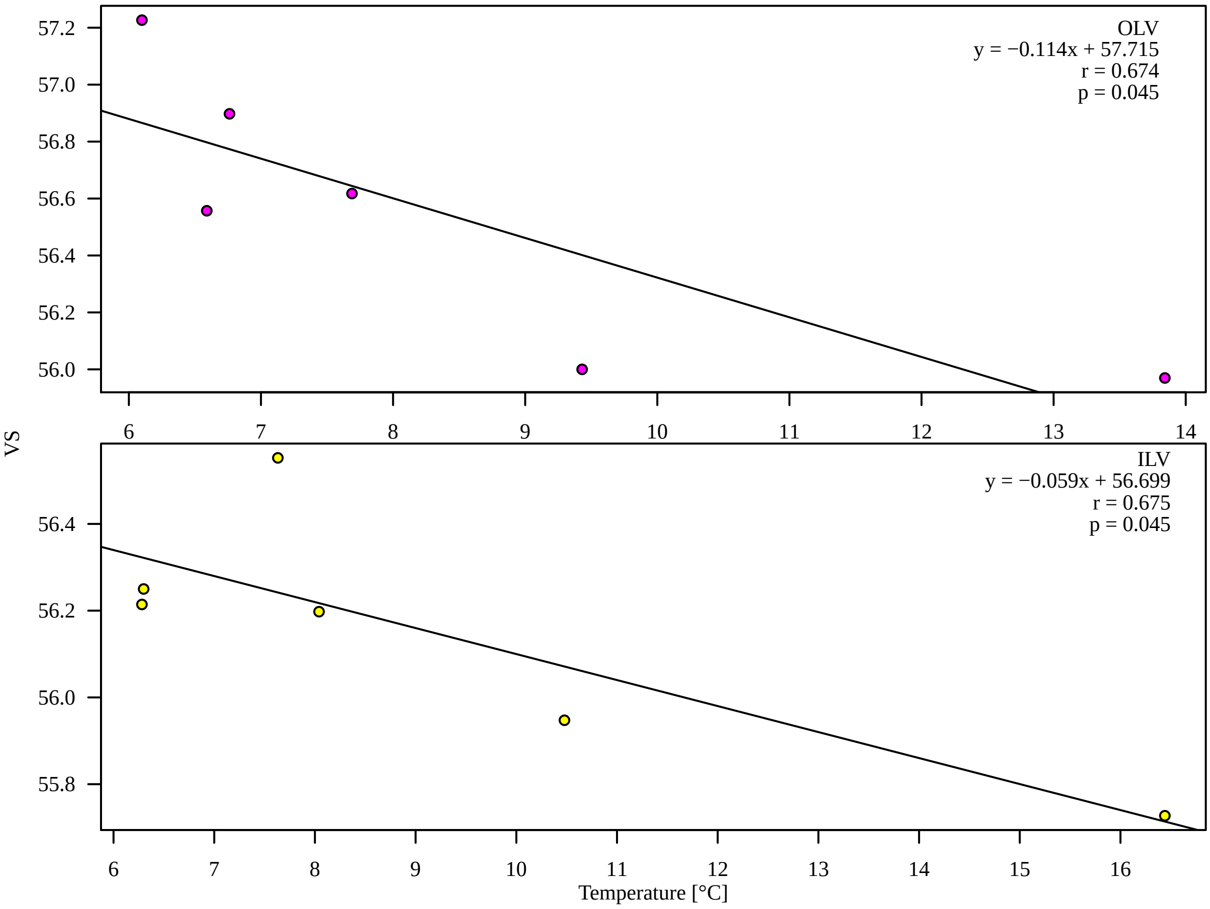

Figure 41: Regression of VS versus temperature for herring typed as OLV and ILV at a depth of 5 m in Strandfjorden and 3 m in Landvikvannet for each sample during the spawning season 2012.

4 DISCUSSION

Based on analyses of population structure, growth, maturation, spawning time and migration at three different scales, the present thesis shows evidence for high population dynamics occurring in Atlantic herring along the Norwegian south coast. Firstly, historical data from 1970–2012 demonstrated inter- and intra-annual stability in population structure and growth in the North Sea, whereas the data were highly dynamic in the Skagerrak/Kattegat as well as in the coastal and local areas studied. These historical data on population dynamics were not influenced significantly by data on changes in environmental conditions, indicating that the most likely explanation to the observations could be historical, seasonal and spatial variability in mixture of populations. There was also evidence in the historic data that mixing of populations during spawning activities potentially could have happened, as a result of the clear overlap in spawning time between herring diverging phenotypically from the west coast, east coast and in the local area. Secondly, this was further investigated with an intensive biological sampling regime in the local area of Landvik and connected fjords during spring 2012. The results of these detailed investigations indicated a mixed presence of three herring types during the spawning period, which differed in terms of otolith characteristics, vertebral count and growth. Thirdly, tracking of individual herring with acoustic tags demonstrated behavioral differences within the local area giving additional support to the hypothesis that herring populations were mixing in the area. In the following a more detailed discussion is given on the results of the analyses of the data from these three different scales with regard to the overlapping herring diverging phenotypically, of potential regular interbreeding and the metapopulation concept.

4.1 From single source population to metapopulation dynamics: the structure of herring in the south of Norway, Skagerrak and North Sea

The historical North Sea data, showing stable meristic characters over many decades, do not allow the unambiguous identification of mixing populations (Figure 42). Therefore the existence of 1 single source population in the North Sea, as suggested by Mariani et al. (2005) throughout genetic differentiation, can be supported. Mariani et al. (2005) demonstrated genetic differentiation through isolation-by-distance between spawning aggregation in the North Sea versus aggregations in the English Channel (Downs) and samples collected along the south coast of Norway. Also morphological differences between spawning herring in the Downs and the North Sea have been demonstrated (Zijlstra, 1969). Downs herring, spawning outside of the study area and entering the North Sea on their routes to overwintering areas, have minor impact on herring in the North Sea, but they can explain the differences between the northern (NNS) and southern North Sea (SNS). Also the occurrence of nursery areas in the southeastern North Sea (Cushing, 1967) explains the significant lower length and age, but similar VS of NNS and SNS herring. Consequently those herring are managed as a single stock called North Sea Autumn Spawners (NSAS).

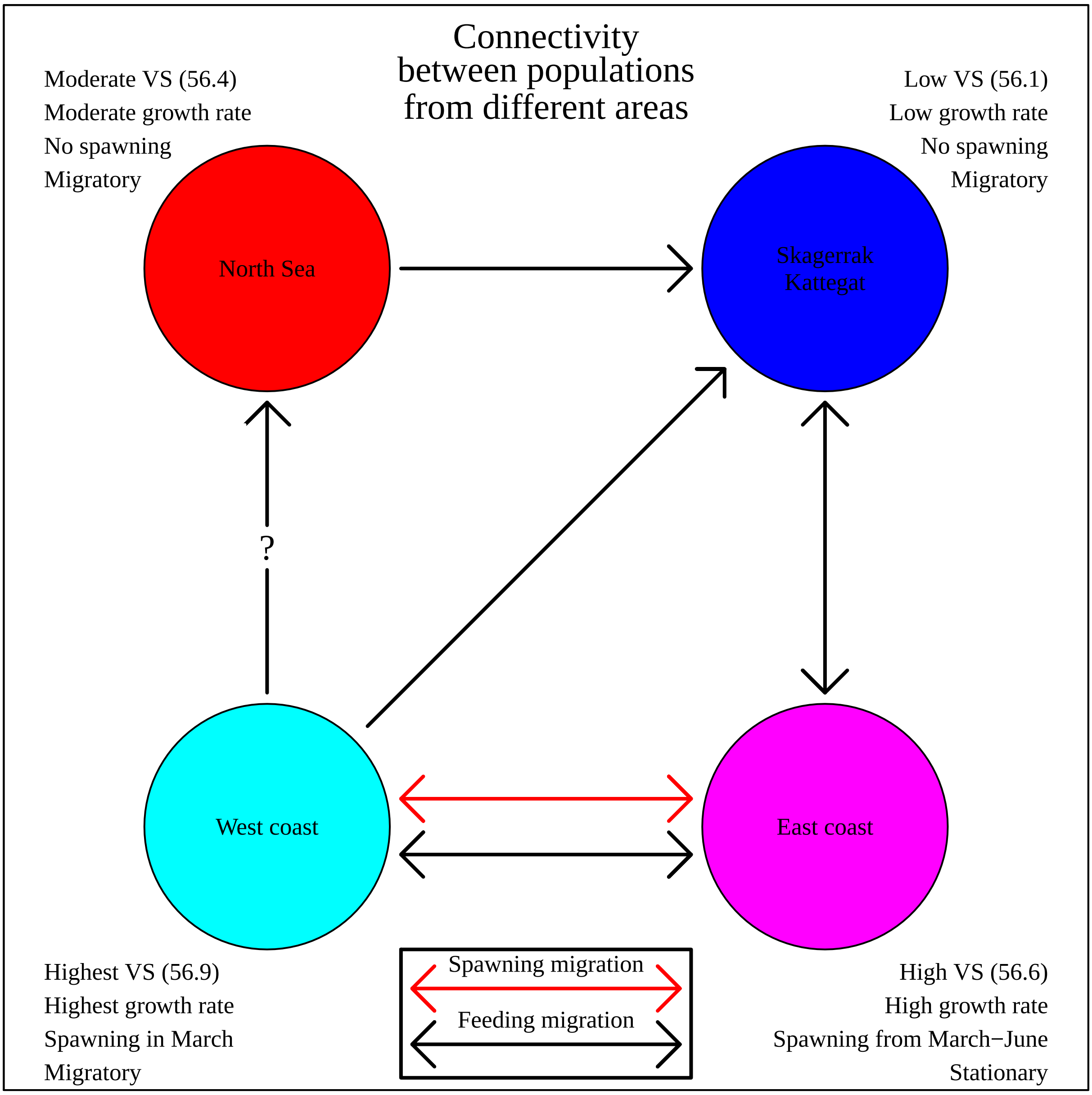

Figure 42: Schematic model of connectivity between herring population from different areas.

The sustained low recruitment in the North Sea from 2002 until recent time, which was explained by Corten (2013) as a regime shift in the ecosystem or predation on larvae by the adult stock, is most likely the reason for the increasing age in NNS after 2000 and the last presence of strong year classes in 1999 and 2001. An alternative explanation suggests a change in the migration routes of Norwegian spring spawners (NSS). Prior to the collapse of NSS in the late 1960s, herring migrated from their wintering areas along the southern border of the east Icelandic Current towards the Norwegian coast (Dragesund et al., 1980). After the collapse NSS were confined to the coastal areas of western Norway. Posterior to the recovery of NSS the migration extended farther out from the coast to the more central part of the Norwegian Sea (Dragesund et al., 1997). Also spawning was observed in 1989–95 at the traditionally spawning grounds south of Bergen (Johannessen et al., 1995). This development of the annual migration of NSS back to the traditional wintering areas along the Icelandic Current, may explain the increasing age in the NNS when older Norwegian spring spawners migrate through the NNS. Also the variation with high VS in February supports this explanation. However, the constant VS for each year in the total data material, even within each year class, and the low inter-annual variation of mean length for herring from the NNS, indicate that the biomass of NSS entering the area must have been negligible.

In contrast to the North Sea, clear evidence of mixing populations in the Skagerrak and Kattegat (SK) was found (Figure 42). The evidence was based on the highly inter- and intra-annual dynamics of population structure, especially with regard to vertebral counts (VS). In the transitional zone between the North Sea and the Baltic the salinity varies from a full marine scale at 35‰ in the North Sea to close to zero in the Baltic Sea. Moreover, the temperatures differ substantially during spawning, as the climate is more stable in the North Sea in autumn than in the Baltic Sea in spring. Such a major environmental gradient influences the development of meristic characters, like VS, during the incubation period and early larval life (Lindsey, 1988; Tåning, 1952). In spite of the extensive mixing of individuals in the transition zone, herring stocks can be distinguished through the exhibition plasticity of meristic characters (Rosenberg and Palmén, 1982). Differences in growth, migration and spawning behavior describe the different stock units (Iles and Sinclair, 1982), in addition to the morphology.

The length and age data of SK herring were similar to herring in the SNS, while VS were significantly lower in the SK. The data clearly revealed a mixture of Western Baltic Spring Spawners (WBSS) and NSAS. For example the mean VS of herring collected in SK was below the NSAS (56.4), but above VS of WBSS (55.8), which is in accordance with findings in other studies (Gröger and Gröhsler, 1995; Hulme, 1995). Also the intra-annual variation of VS and within a year class fluctuated between those two means, indicating an occurrence of NSAS during the first three months of a year, followed by the occurrence of migrating WBSS to their feeding areas. In addition, the observed dynamics in VS could include a mixing of local spring spawners with NSAS and WBSS, which normally takes place during spring and summer within the Skagerrak(Biester, 1979; Johannessen et al., 1995; Rosenberg and Palmén, 1982).

The occurrence of WBSS in the study area during summer can be traced in both North Sea areas, when samples with VS lower than 56.0 were found in both areas in June-July. While the occurrence of WBSS has almost no impact in the NNS, it influenced the results of herring collected in the SNS. Also it seems like that SNS is a mixture between NNS and SK, as it was not as stable as the NNS, yet not as dynamic as the SK. For example the inter-annual variations in length were clearly lowest in NNS and highest in SK, whereas the comparative variation in SNS was more intermediate. This indicates that the majority of herring collected in SNS where originally NSAS, whereby WBSS dominated in samples collected in the SK, as suggested by Ruzzante et al. (2006). Still, no clear evidence of spawning was found in the biological samples from the oceanic areas, which probably can be explained by very low sampling effort on the spawning grounds during the spawning season; i.e. the Norwegian fishery for herring in the North Sea normally occurs outside the spawning season and areas, and IMR does not conduct surveys overlapping with spawning activities in these areas. However, recent studies have shown significant genetic differences between NSAS and WBSS, suggesting that the salinity is the major isolating barrier (Bekkevold et al., 2005). Still, adult herring are known to tolerate a wide range of salinities from 6‰ up to 40–45‰ (Holliday and Blaxter, 1961). Also herring live in more extreme salinities like lakes (Hognestad, 1994; Neb, 1970), but for successful reproduction saline water is required. Salinity is therefore suggested to play a major role in the differentiation of these two stocks in the spawning areas. Although the mixing of populations occurs during feeding season, there is not necessarily any connectivity in a genetic sense (Stephenson et al., 2009). Therefore, the mixing of NSAS and WBSS in the SK does not support the metapopulation concept.

In contrast to the stable ecosystem in the oceanic North Sea and the mixing of herring in the Skagerrak without supporting the metapopulation concept, the historic data also showed that mixing of herring populations occur along the south coast of Norway with indications of metapopulation dynamics (Figure 42). Despite the differences in growth, length, age and VS between the east (EC) and west (WC) coast, the similar trends of inter-annual changes in these parameters suggest that migratory herring visit both coastal areas during spring. The immigrating herring are most likely NSS, while the second component may be a more stationary coastal Skagerrak spring spawning (CSS) population. The occurrence of herring with high VS, above 57.0, combined with high growth along WC is normally an indication of migratory NSS entering the area (Runnstrøm, 1941a). NSS reappeared at their spawning grounds south of 62° N in 1989, after abandoning the area in 1959 (Johannessen et al., 1995; Røttingen, 1989). This is in accordance with the results of the present thesis demonstrating that the VS increased in WC in the 1990s indicating that a significant amount of NSS migrated south of 62° N during this period. In addition, the VS along EC also increased after 1989, indicating that the migration of NSS may have continued well into the Skagerrak area. Still, it seems that the changes along WC were due to the appearance of NSS solely, while the changes at EC probably were a mixture of variations in the oceanic areas and occurrence of immigrating NSS. Until 1999 the population structure of EC herring was quite similar as in the oceanic areas. However, in the new millennium after the appearance of the 1998 year class, the only strong year class in the EC, the population structure became more similar to that observed in WC herring. Albeit the effects of immigrating NSS were lower in EC than WC, which indicate a higher fraction of coastal herring. Also the intra-annual variations indicate higher abundance of herring with lower VS in EC, compared to herring from WC. Moreover, the different maturation stage composition observed between WC and EC herring revealed the influence of NSS in WC. In WC spawning mainly occurred during March as also observed with NSS south of 62° N by Runnstrøm (1941a) and Johannessen et al. (1995), whereas in EC spawning took place from March until May. The overlap in spawning time is a prerequisite for the existence of metapopulations (McQuinn, 1997). Cross-fertilization between herring from WC and EC could not be observed directly, but the historical data clearly demonstrate an overlap in spawning period in March, which at least prove a potential mixture during spawning between herring diverging phenotypically in these areas. The intra-annual changes in VS in EC indicate the appearance of another population than NSS and CSS in the area. While VS decreased constantly from January until December in WC, there was a clear decreased VS during May-August in EC as seen in the Skagerrak area due to the entering WBSS (Ruzzante et al., 2006). While the effect of WBSS was visible in EC from May-August, it was only visible in WC in July. However, this mixture does not support the metapopulation concept because no spawning occurred in WC at all, and only during May in EC. The potential overlap in spawning between coastal herring and WBSS is negligible, because WBSS herring start their migration into the SK and westwards after spawning in the Baltic around the island of Rügen using the SK only as important feeding ground during summer (Aro, 1989; Biester, 1979; Weber, 1975).

To sum up, the data on inter-annual and between year classes changes in VS and growth were independent on environmental effects like salinity and temperature. Hence, the observations of herring diverging phenotypically in samples along the south coast of Norway clearly indicate a mixture of at least 2 different herring populations in the area. The observed overlap in spawning activities in March between the herring diverging phenotypically in EC and WC, suggest that metapopulation dynamics potentially may have happened, and that there would be need for more detailed data on the subject before concluding. The detailed data on population dynamics at the south coast will be discussed the following.

4.2 Evidence of the metapopulation concept? An approach of interpreting the dynamics in Landvikvannet and the connected fjords

The detailed biological sampling during the 2012 spawning seasoned revealed that similar high dynamics in herring population structures as observed in EC and WC can be observed in the local area of Landvikvannet and the connected fjords. In this area three herring components could be identified by diverging otolith characters, growth, VS, stage of maturity and reproductive effort (Figure 43). It is assumed that three components that were present in the local area were NSS, true Landvik herring and CSS. The spatial and temporal overlap during spawning of different populations as required by the metapopulation concept according toMcQuinn (1997) is fulfilled in the local area of Landvikvannet and connected fjords. The two spawning populations normally found in this area, Landvik and CSS herring, as well as the migratory NSS herring were all found to overlap in spawning stages despite different timing of peak spawning; i.e. they were caught in the same gillnets at the same time with running gonads. This is as close to an evidence of mixing during spawning one could get, but as long as the cross-fertilization between herring could not be observed directly one cannot rule out that the populations might separate during the actual spawning events. No larvae or eggs were found during investigations with plankton nets or scuba divers in Landvikvannet in June 2011; the only proof of spawning in Landvikvannet was two eels with fertilized herring eggs (Figure 44) caught in the same gill nets as herring with running gonads. In 2012 there was also one attempt with plankton nets and skin diving in Strandfjorden, in the

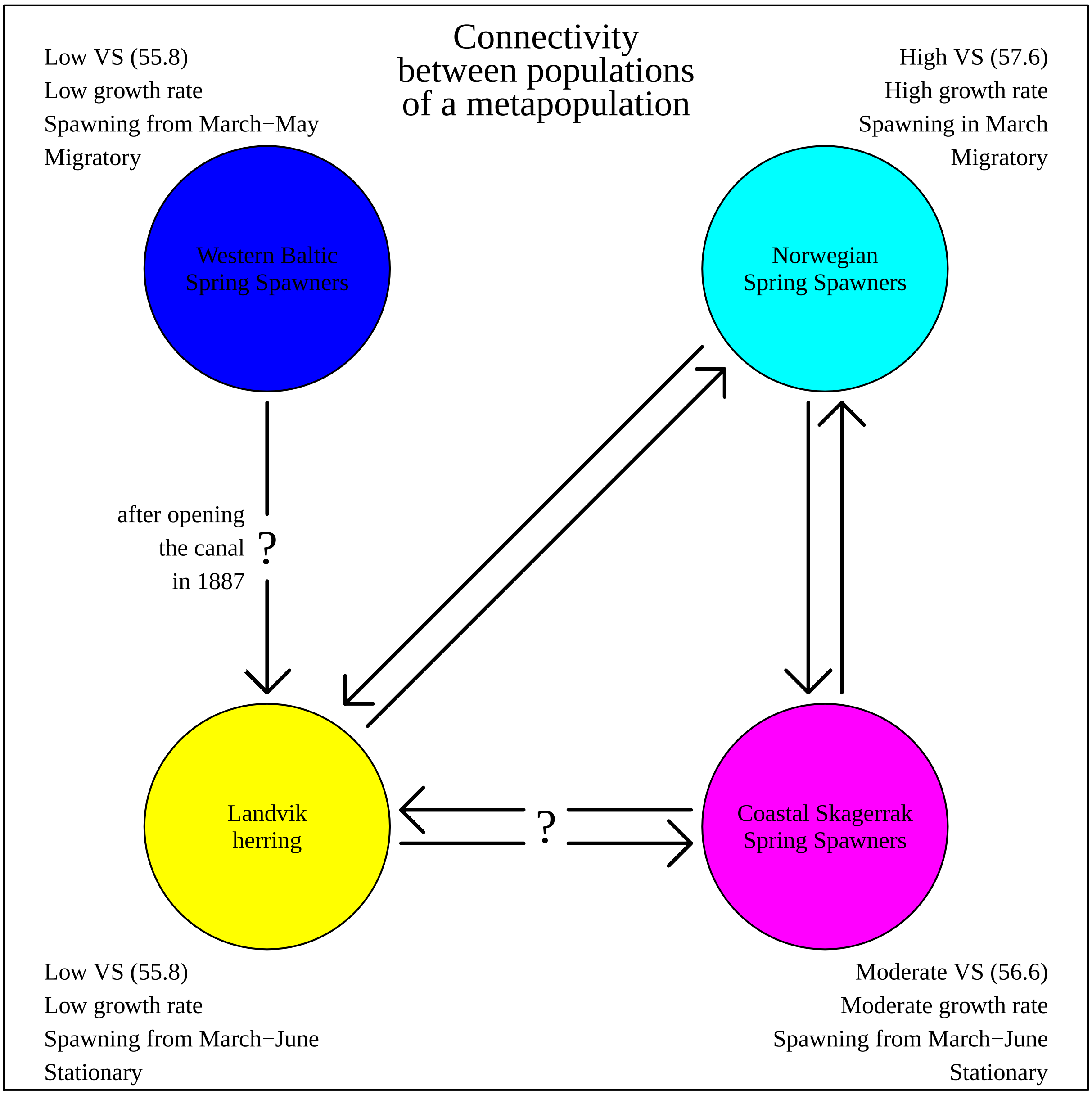

Figure 43: Schematic model of connectivity between populations of a metapopulation in the local area of Landvikvannet and the connected fjords. Western Baltic spring spawners are given to demonstrate possible origins of Landvik herring.

area where schools were observed acoustically at the entrance of Reddal canal, but neither eggs nor larvae were found. Still in 2012 in both ecosystems there was a predomination of herring with running gonads, and spent herring were also observed. Therefore spawning is expected to have happened somewhere in the local area, and one have concluded that more effort is needed to find the spawning spots and hatched larvae. Regardless of the known selectivity of gillnets (Hamley, 1975) and the possible shifted length and age distribution the discussed population structures and dynamics are not supposed to be affected. All used gillnets, both in Landvikvannet and the connected fjords as well as in other areas, had always the same mesh size of 26–29 mm or similar and therefore the shift in length and age distribution was the same for all collected samples. Due to the selectivity of gillnets the estimated growth curves of herring might be influenced and do not represent the original growth, but the

Figure 44: Eel caught in Landvikvannet in 2011 with fertilized eggs in the stomach.

differences between the single populations are not affected as long as the same mesh size was used always. Consequently no indirect estimations of length distributions are needed as supposed by Winters and Wheeler (1990). Also gillnet catches can be used as an estimate of fish abundance and would reflect the true population size of different herring (Hansson and Rudstam, 1995).

NSS herring was present in both ecosystems, and was split from CSS and Landvik herring based on the otolith characteristics, and confirmed with high VS. After splitting out NSS, there was still a clear difference in VS between CSS and Landvik herring. The differences in VS, which are formed at very early stages (Pavlov and Shadrin, 1998), reflect the origin of the fish at spawning. The number of vertebrae are modified by the environment in a way of a positive correlation between salinity and VS (Hempel and Blaxter, 1961), in contrast the temperature correlates negatively with the mean vertebral counts (Hulme, 1995; Johnston et al., 1997). In this case the warmer Landvikvannet and the lower salinity compared to Strandfjorden could explain the low VS of Landvik herring compared with CSS herring. This could also imply that CSS and Landvik herring in fact utilize different spawning grounds and therefore are reproductively isolated. On the other hand, the significant correlation of increasing temperature and decreasing VS among Landvik and CSS herring in 2012 may indicate that herring in fact home to this local area and even return to spawn at same the time as their parents spawned; i.e. herring hatched in May would also have a tendency to spawn in May, whereas herring hatched in March would tend to spawn in March. This has been proved in summer-autumn spawning herring in northern Norway

(Husebø et al., 2005). If this is the case, one would expect that herring found in Landvikvannet and connected fjords with running gonads to have high VS in March and low VS in May-June due to the increase in temperature as observed in 2012. Moreover, this could mean that the Landvik and CSS herring, which differs in VS, in fact use the same spawning grounds, and are only split by spawning time. Still, the fact that the growth and asymptotic length increased with VS and decreased with spawning time, both inside and outside Landvikvannet, suggest that the Landvik herring and CSS herring may not overlap during the nursery period and at adult feeding grounds. This may be two populations with different spawning time, VS and growth, that home to the same area and partly overlap during spawning, whereas they may not necessarily mix for the rest of the year. If we assume homing in herring, we have to distinguish between natal homing (philopatric) and repeated homing (Horrall, 1981; MacLean and Evans, 1981). The principle of natal homing is central to the discrete population concept (Iles and Sinclair, 1982). In herring high (75–95%) returning rates of adult herring to spawning areas could be demonstrated (Hourston, 1982; Wheeler and Winters, 1984), but this results from tagging experiments did not demonstrate necessarily natal homing. Moreover, recent genetic studies supported the natal homing of herring in the North and Baltic Sea (Gaggiotti et al., 2009; Ruzzante et al., 2006). Likewise Brophy et al. (2006) indicated that spawning season and location of Atlantic herring are predetermined and not learnt from repeated spawning. Although the spawning site selection of herring can vary inter-annually (Haegele and Schweigert, 1985). In this study natal homing to spawning grounds within the local area is suggested in Landvik herring and at least repeated homing for CSS (maybe also natal homing), but the results did not support homing for NSS. The high abundance of 3 year old NSS and the missing individuals older than 8 years and the stability of morphometric and meristic characters indicate an independent selection of the spawning ground which is supported by Slotte and Fiksen (2000). Despite the suggested homing of CSS and Landvik herring the metapopulation concept can be still supported (McQuinn, 1997). Besides homing, straying from natal spawning grounds is relatively common for herring and therefore demonstrate considerable gene flow (Hourston, 1959; Smith and Jamieson, 1986). Thorrold et al. (2001) demonstrated spawning site fidelity of 60–81% in a metapopulation of weakfish (*Cynoscion regalis*), where also straying appeared between different spawning sites. Even Brophy et al. (2006) results showed a switching of spawning season below 10%, facilitating gene flow.

Even we could not observe the actual spawning event, neither in Strandfjorden nor in Landvikvannet, do our results demonstrate an unambiguous appearance of two during spawning isolated populations. The most important character to identify the populations, the vertebral number, can be explained by the low salinity and warmer temperatures in Landvikvannet. The correlation found between temperature and VS during 2012 were only found at a certain depth in each ecosystem; 3 depth in Landvikvannet and 5 m depth in Strandfjorden. Both depths probably indicate the potential spawning depths in the two locations. In Landvikvannet the depth of 3 m can by unequivocally explained by the depleted oxygen and the occurrence of H_2S, also herring schools could be observed at a depth of 3 m with an echo sounder in 2010 (Figure 45). In Strandfjorden the conditions of the spawning ground change below 5 m depth, where the bottom becomes more sandy and muddy, whereas above this depth there are stones and rocks with seaweed, which are known to be preferred as spawning substrate of herring (Runnstrøm, 1941a).

Despite the suggested reproductive isolation of CSS and Landvik herring, they can be regarded as subpopulations within a metapopulation with NSS. Also there are some indications of potential interbreeding between CSS and Landvik herring, based on the observed overlap of herring in spawning stage as discussed above, and based on current knowledge on how mixed fertilization between herring populations may be successful. As demonstrated by Folkvord et al. (2009), genetic exchange of NSAS and NSS produced viable larvae during the post-feeding stage. Therefore, it would seem unlikely that different spring spawners would meet difficulties in this respect. Besides the viable larvae Folkvord et al. (2009) showed an intermediate growth of those larvae compared to the maternal growth of NSAS and paternal NSS. Also Lambert (1990) identified an intermediate form of otoliths between two different spring spawning herring populations. Even differences in meristic characters of hybrid herring were demonstrated by Hempel and Blaxter (1961), indicating that VS is not depending on environmental conditions solely, but also on heredity. Hence, the mixing of CSS and Landvik herring during spawning and the assumption of gene flow could in fact explain the significant increasing VS observed in Landvikvannet since 1984. The fact that there was an absence of older NSS mixing with

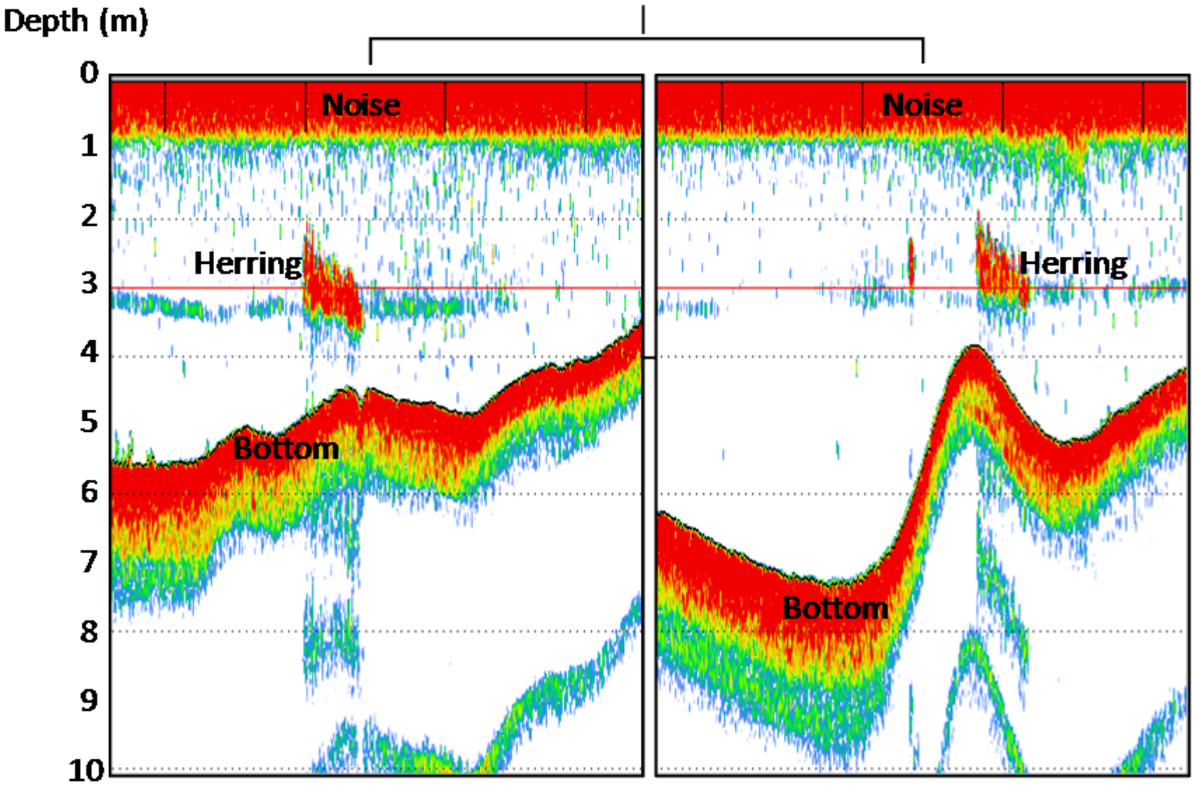

Figure 45: Herring schools at the depth of 3 m observed 2010 in Landvikvannet by an ER60 echo sounder and a transducer at a handheld stick just below the surface.

CSS and Landvik herring in 2012 may be explained by the very special spawning migration of NSS herring in 2009–10. During these two years a significant proportion of the adult NSS chose to migrate south of 62° N, and this led to the largest fishery in the fjords east of the traditional spawning grounds in Karmøy since the 1950s (Directorate of Fisheries, 2013). IMR internal reports demonstrated with sampling that the fishery in fact was on NSS herring based on VS data and growth, but they did not have surveys to prove the actual abundance in the area (Slotte et al., 2009). Still, the fishery and reports from fishermen themselves suggested that the abundance was high (See Appendix Table A.1 for actual numbers). One hypothesis is therefore that the 3 year old NSS observed mixed with CSS and Landvik herring in 2012 was a product of this significant spawning at southern grounds in 2009. It is common that first time spawners of NSS find their first spawning ground at random if they do not meet older conspecifics and learn their way to the spawning grounds and wintering grounds (Huse et al., 2010; Slotte, 1999b, 2001). It is also common that NSS herring tend to migrate upstream to spawn (Slotte and Fiksen, 2000), and hence it is likely that the NSS growing up in Boknafjorden or further south as a result of the 2009 spawning, may have chosen to spawn close to the nursery areas and even migrate further upstream south-east against the coastal current to spawn, and as a result ended up in Landvikvannet and connected fjords.

Another additional explanation for the absence of older NSS mixing with CSS and Landvik herring in 2012 could be related to size and schooling. Because schooling demands a certain degree of size-matching among individuals (Pitcher et al., 1985), the selection of younger NSS may be based on their size. The degree of size-matching in schools is related to the effective anti-predator behavior of schools (Nøttestad et al., 2002)and the unequal swimming power of siblings of different size (Nøttestad et al., 1999), whereas the first argument may be neglected in case of this local area. With the age of 3 years NSS are probably first-time spawners, growing up in southern nurseries as a result of the 2009 spawning events, which may adopt the behavior of the joint local populations they mix with during the nursery period as postulated in the adopted-migrant hypothesis (Corten, 2002; McQuinn, 1997).

Also we assume that CSS and Landvik herring represent more stationary populations not conducting oceanic migrations, whereas NSS is known as a migratory population with decreasing energy loss during migration with size (Slotte, 1999a). The higher investment in growth of NSS, comparatively to a stationary population, seems more advantageous to increase migration potential because the optimal swimming speed increased (Winberg, 1961) and metabolic rate decrease with body size (Ware, 1978). Additionally the low investment in reproduction (low GSI and gonadK) of NSS compared with the investment of CSS and Landvik herring supports the assumption of one migratory and two stationary populations. Similar observations were found by Silva et al. (2013) comparing local populations along the Norwegian coast with NSS.

Despite the indicating results of high reproductive investment and low growth for CSS and Landvik herring as stationary populations, it seems that they are not as stationary as other local herring populations, like Trondheimsfjord or Lindås herring, which can be observed throughout the whole year at their local areas (Broch, 1908; Johannessen et al., 2009; Lie et al., 1978; Runnstrøm, 1941b). Intra-annual changes of length, age and VS in the local area indicate migrations of all three components. The first present components, already in February, were herring outside Landvikvannet (OLV) and NSS, whereas more than 80% were OLV herring. While OLV herring were present until June and almost equally abundant, NSS left the local area in May with the clear peak in March, when almost 50% of all caught NSS were present. The first herring being present inside Landvikvannet (ILV) appeared in early March (≈2%), with an increasing tendency and peaking in May. Still some individuals of ILV were present in August. The high abundance of NSS in the end of March influenced the meristic characters of both OLV and ILV, suggesting that not all true NSS could be identified through otoliths reading, which is indicated through the increasing VS with increasing length of OLV and ILV herring. Therefore the identification of OLV and ILV into CSS and true Landvik herring needs to be done with some caution, as long as unidentified NSS are still present in OLV and ILV herring. Also the decreasing VS of OLV may be an indication of the appearance of true Landvik herring in the connected fjords. All in all the identification of the different components in the local area need more investigations to be more precise. One method to study this in more details is to track the individual behavior with telemetry data, which was conducted in 2012 and is discussed below.

4.3 From individual behavior to population structure, the use of acoustic telemetry

Acoustic tagging of herring is a suitable method to understand the relationship between the individual level as well as the interactions between different populations (Langård et al., 2012), and it was used in the present study to explore if the herring visiting Landvikvannet and connected fjords would have diverging behavior, which could indicate that they were from different populations and mixing in the area. The original plan of tagging herring inside Landvikvannet could not be fulfilled; therefore we tagged herring in Strandfjorden instead, where herring schools were visible on the echo sounder and were biting and jigging on hook and line. The absence of herring schools in Landvik, which could not be seen on the echo sounder, hindered the catching of herring with line and hook in this area, even trials were carried out with no success. Schools as observed acoustically in Landvikvannet in 2010 were not observed in 2012. The time of the first tagging experiment, in the end of March, was not the most suitable as the historic data on Landvik herring were collected in May, and as the biological sampling in 2012 demonstrated that peak spawning of Landvik herring in fact was in May. However, even in May and June, we were not able to catch herring in Landvikvannet, also using a beach seine. These observations indicate that herring enter Landvikvannet more on the individual level, instead of at a school level; at least the schools are not very big. In fact, in the Reddal canal we did observe herring swimming upwards in groups below 10 individuals. However, outside the canal in Strandfjorden the herring were observed in more dense schools. , During biological sampling more than 600 individuals were caught in Strandfjorden in one gillnet compared with a maximum of 170 herring in Landvikvannet in one gillnet, indicating that herring enters the lake in smaller groups. On the other hand, in 2010 they caught 1000 herring in one net in Landvikvannet, suggesting that even though they enter the lake in small groups they at least may appear in high abundance in the lake. One explanation of why the herring enter the canal and lake in small groups may be antipredator behavior. Clearly the canal is very shallow, and large schools would be very visible from the air for hunting birds (Axelsen et al., 2001; Mackinson, 1999). The herring tagged in the present study showed three different behavioral patterns during their period inside the monitoring system, the local area of Landvikvannet and the connected fjords. Besides herring entering Landvikvannet, two different types of behavior could be observed; migratory and stationary behavior. While some individuals left the monitoring system within one week directly to the open sea (migratory), others stayed and migrated inside the system (stationary). One assumption is that the migratory herring represent NSS herring and the stationary herring representing a mixture of CSS and Landvik herring. Probably NSS spawned directly after tagging in Strandfjorden and started their annual migration. If they plan to join the rest of the NSS herring they would have had to migrate west and northwards towards the Norwegian Sea. Among the stationary herring, one could differentiate between CSS and Landvik herring. Both left Strandfjorden after tagging, but stayed inside the monitoring area. One interpretation of the data is that post-spawning herring aggregated in Bufjorden where they probably searched for food, while pre-spawning herring migrated between Strand- and Bufjorden waiting for the right spawning wave (Lambert, 1987; Popiel, 1958). After the potential spawning in Strandfjorden CSS stayed in Bufjorden before the left the monitoring area, indicating that CSS aggregate in schools during spawning as well as feeding.

Although herring entering Landvikvannet stayed in Bufjorden before they started their migration. The behavior was similar to CSS herring, except for the actual migration into the lake. Due to the low number of receivers in the lake we were unable to observe the behavior of tagged herring inside the lake. Also the locations of the receivers were not suitable, it would be better to moor the receiver units more apart from each other. Then a bigger area could be observed. However, Landvik herring migrated inside the lake for up to 36 days and did not stay at the beginning. After leaving the lake they swam directly into Bufjorden, similar to CSS with Strandfjorden. Hence, it is assumed that those herring in fact spawned in Landvikvannet, even though biological proofs of spawning products are lacking up to date. Also a higher fraction of tagged herring in May entered Landvikvannet, which also indicated that they reach the area later in the season than NSS and CSS herring.

The migration of both, Landvik and CSS, appeared mostly during the night. Normally spawning herring aggregate in schools during daytime in pelagic waters to avoid predation (Axelsen et al., 2000; Nøttestad et al., 1996) and as soon as the darkness arises herring begin their vertical migration (Blaxter and Parrish, 1965; Woodhead and Woodhead, 1955). But in shallow waters, as in the local area, spawning herring may stay in touch with the bottom at all hours and did not disperse closer to the surface during darkness (Slotte, 1998). Also small schools may split from the large aggregation for spawning and migrated to their spawning grounds (Johannessen et al., 1995; Skaret et al., 2003), which are suggested in Strandfjorden or Landvikvannet. After spawning they may join again the bigger schools in Bufjorden, before they start their migration towards feeding grounds, as suggested in other shallow areas (Nøttestad et al., 1996). Opposite to NSS, which probably migrate to feed in the Norwegian Sea, it is assumed that CSS and Landvik herring most likely feed closer to the study area along the coast of southeast Norway.

The assumption of coastal feeding of CSS and Landvik herring was supported through the second monitoring system in Sømskilen. Instead of migration south-westwards towards the Norwegian Sea, some individuals migrated north-eastwards. In addition, the telemetry data demonstrated that they stayed along the coast instead of migration into open sea of the Skagerrak or southern North Sea. Furthermore, some individuals stayed for longer time in Bufjorden or migrated inside the monitoring system, indicating a stationary behavior also during the feeding. Hence, the telemetry data indicate a differentiation between NSS, CSS and Landvik herring in the study area through behavioral patterns. Additionally potential spawning events could be observed through migratory behavior inside the monitoring system. To demonstrate the affinity of CSS and especially Landvik herring to this local area, we assume a high returning rate of those tagged herring in the next spawning season 2013. This remains to be analyzed, and is not included in the present study.

4.4 The effect of environmental conditions on the population structure

The most important factor influencing the phenotypically diverging herring populations is salinity. In the local area two different ecosystems exist, while the connected fjords can be compared with environmental data from the open sea, like the North Sea, environmental data of Landvikvannet can be compared with a more brackish environment like the Baltic Sea. Those differences can be observed between the two populations in the local area, especially in terms of VS and growth. Also the anoxic water layer of Landvikvannet is comparable with the Baltic Sea. The variable depth of the depleted oxygen concentration in Landvikvannet complicates the spawning of herring. By selecting the optimal spawning substrate and depth Landvik herring have to ensure sufficient oxygen concentration to risk no egg mortality due to anoxic conditions. Therefore herring need to have a good timing in spawning to guarantee the survival of their offspring.

Testing the influence of temperature and salinity along the south coast of Norway and Landvikvannet on growth and VS of corresponding herring did not show any significance. However, this indicates that herring of different origins mingle in the local area during spawning. In general the growth is influence by temperature (Husebø et al., 2007), additionally parental effects occur on growth (Folkvord et al., 2009). Normally the most important factor influencing growth is prey concentration (Folkvord et al., 2000, 2009; Kiørboe and Munk, 1986). Since we assume mixed spawning of different herring components in the same area the prey availability should be the same and can be neglected. Hence the required gene flow of the metapopulation between different components can be warranted in the local area; as long as the growth is not influenced by temperature it must be dependent on genetics.

4.5 The metapopulation concept in marine environments

The present results on metapopulation dynamics in herring is supported by a wide range of studies on both Atlantic herring (Johannessen et al., 2009; McQuinn, 1997), northern cod (*Gadus morhua*) (Smedbol and Wroblewski, 2002), weakfish (*Cynoscion regalis*) (Thorrold et al., 2001), or walleye pollock (*Theragra chalcogramma*) (Bailey et al., 1999), also along coral reef fish (Man et al., 1995; Saenz-Agudelo et al., 2012), estuarine or diadromous fish (Jones, 2006), invertebrates, plants or algae (Kritzer and Sale, 2006). Even the number of metapopulation concepts is increasing in the marine population dynamics and genetics literature, its applicability to marine systems is still debated (Smedbol et al., 2002). Also the definition of metapopulations can vary by different authors (Kritzer and Sale, 2004), for example in the definition of Hanski and Simberloff (1997)the exchange among subpopulations is already sufficient. Therefore scientists need to define the term metapopulation and use appropriate citations to avoid the potential for misleading conclusions. In the case of northern cod for example, Smedbol and Wroblewski (2002) applied the more relaxed definition of Hanski and Simberloff (1997) to demonstrate metapopulation structures. Whereas northern cod would not be considered as a true metapopulation under the definition of Smedbol et al. (2002). Hence, in a broader aspect the results of the present study on metapopulation dynamics in herring are clearly contributing to the ongoing discussion on the subject.

4.6 Management implications, in the case of existing metapopulations

A basic concept in the assessment of marine fisheries that enables fishery management is the multigenerational return by adults to a specific spawning ground to be scaled appropriately to underlying population production rates (Secor, 2005). Also the diversity of spawning components, especially the maintenance of stationary and local populations, is considered to be an important target in fishery management, particular in herring fisheries (Bierman et al., 2010; McPherson et al., 2001; Smedbol and Stephenson, 2001; Stephenson et al., 1999). Higher rates of connectivity through straying and entrainment influence the internal metapopulation dynamics in case of persistence and stability (Secor et al., 2009). Therefore a research priority in management should be the connectivity to protect the components of a metapopulation and their essential habitats. However, along the Norwegian coast it is hypothesized that many potentially genetically unique populations with phenotypic adaptations to a stationary life exist in well-defined environments with certain rates of connectivity (Husebø et al., 2005; Johannessen et al., 2009). As direct contributions to the biodiversity along the coast of Norway these stationary populations, including

CSS and Landvik herring, need to be included in the management of herring, especially in the territorial waters of Norway.

Moreover, the biological impacts on mammals, birds, fish and other organisms that prey upon the egg, larvae, immature and adult herring in the local areas are enormous. The understanding of the distribution of both genetic and phenotypic diversity is essential to prevent the extinction of local populations through overfishing. Commercial fishing may not be the problem of Landvik herring, but the population of CSS along the Skagerrak should be included in management to maintain biodiversity. The mixing populations in coastal waters can deplete the small and stationary populations by large-scale mobile fishing effort which is intended to fish on large oceanic populations (Iles and Sinclair, 1982). Therefore the difficulties for fishery management of mixing populations during their annual migration are to prevent disproportional fishing effort on small and stationary populations and the overexploitation of local populations. Kell et al. (2009) simulated the long-term management of a metapopulation showing that lumping of different populations will underestimate the risk of a collapse and overestimate the probability of recovery.

Managing exploited fish in a metapopulation context requires extensive assessment of population size and demography, connectivity, genetics and estimation of mortality (Jones, 2006). If herring in southern Norway should be managed by using the metapopulations concept several barriers must be resolved, whereas the most important is to determine local population size. Fisheries management would reinforce finer scale regulations and the harvest of herring need extended supervision. So far it could not be proven if those fine scale regulations are necessary for the maintenance of biodiversity. Do local populations extinct or can they recover? If so, should fish be managed as parts of a metapopulation or is the management of mixed-populations sufficient? Therefore further studies should concentrate on the replenishment of local populations through straying and migrations from other populations after strong impact of harvesting.

However, the actual knowledge about the dynamics in herring would recommend management of the metapopulations concept to avoid the depletion of local populations due to large scale regulation. Secor et al. (2009) suggest several management strategies to stabilize metapopulations, in the case of reducing the degree of dominance as well as the covariance in the target metapopulation. One example of a successful strategy could be the ‘in-season, survey, assess, then fish’ protocol by Stephenson et al. (1999) which has its purpose to account for both spatial and temporal distribution. This management tool is the first to consider local populations in the management. Still this tool should be used precautionary in the management of herring along the south coast of Norway to avoid the consequences of making an erroneous assumption. For example could the false assumption of connectivity, as required in a metapopulation, in the case of the existence of discrete populations lead to overexploitations, whereas assuming discreetness when there is connectivity would have no consequences (Stephenson et al., 1999).

4.7 The status quo of the Landvik mystery

During the detailed study in 2012 we clearly demonstrated high dynamics inside Landvikvannet rising up with the question of the origin of this population. There are two possible explanations. The first explanation assumes that original CSS herring entered the lake after the opening of the artificially Reddal canal in 1877 for spawning. Due to the lower salinity and higher temperature in the lake the juvenile herring developed those significant diverging characters. A strong natal homing effect of herring would lead to the development of a new local population inside Landvikvannet. Nævdal (1972) came to the conclusion, however, that less than 100 years are sufficient to develop distinctive characters and genetics for a population. Also Neb (1970) demonstrated that this time interval and the differences in salinity are sufficient for herring to diverging in meristic characters. However, this explanation assumes reproductive isolation during spawning between the original CSS herring and the newly developed Landvik herring.

Another explanation of the origin of Landvik herring might be the colonization of WBSS herring in the lake after opening the canal artificially in 1887 (Figure 43). First-time or even repeated spawners could have established Landvikvannet as new spawning ground. The reason for WBBS not to conduct their annual migration to the original spawning grounds off the island Rügen may be a trade-off between survival of progeny and physiological migration constraints, as shown for NSS by Slotte (1999b). Therefore WBSS with weak conditions stayed close to their feeding ground in the Skagerrak and found by accident Landvikvannet, which had similar environmental conditions than their original spawning ground. Within the next generation the homing effect, back to Landvikvannet, was much stronger than joining their conspecifics back to the island Rügen. Huse et al. (2010) demonstrated that a high ratio of first-time spawners could lead to establishment of new wintering grounds, in the case of Landvik herring, it may lead to a new spawning ground. Supporting those two explanations is the lack of documented presence of herring before the opening of the canal. The first observation of herring was made around 1900 (Knut Hansen, pers. comm.).

However, independent of the origin of this local population, further investigations are necessary to solve the dynamics in Landvikvannet. So far it is impossible to identify the purpose of Landvik herring to migrate into the lake at all. For Landvik herring we clearly assume spawning migrations, as the characters are diverging significantly compared with CSS. After the detailed season in 2012 we can withdraw the assumption of a stationary local population inside the lake. Therefore it will be essential to study the migration and behavior of Landvik and CSS herring outside the local monitoring area to indicate similarities or differences. Furthermore herring may use the lake in the case of antipredator behavior, as the results demonstrate that no predators of herring were caught in Landvikvannet. This could be applied for CSS herring also; likewise CSS could enter the lake in the beginning of the spawning season in case of searching the best habitat for spawning. So far the mystery of Landvik herring could not be solved completely, but we gain some deeper insight into the local population of Landvikvannet.

4.8 Further studies

The results of this study certainly require further investigations, firstly to implement a suitable management strategy for the high dynamics along the south coast of Norway and secondly to solve the Landvik mystery. In case of the dynamics along the territorial waters of Norway it is essential to demonstrate what happens after the spawning of NSS. Therefore the population structure of remaining herring must be investigated in more details in cases of analyses of otolith shape (Burke et al., 2008), microstructure (Clausen et al., 2007), core microchemistry (Hatfield et al., 2005), and stable isotope composition (Valle and Herzka, 2008), as a supplement to studies of microsatellite DNA (Bekkevold et al., 2005; Mariani et al., 2005). Those implications of genetics, using microsatellite DNA demonstrated differentiations between Landvik herring (sample from May 2010) and NSS, as well as the local herring populations from Trondheimsfjord and Lindåspollene, Icelandic spring and summer spawners and Faroese and North Sea autumn spawners (Skírnisdóttir et al., 2012). New technologies and methods in genetics, like analyses on Single Nucleotide Polymorphisms (SNPs) (Lamichhaney et al., 2012; Limborg et al., 2012), will probably improve our understanding of herring population structures and demonstrate more differentiation among populations. Selective markers such as SNPs have the potential to reveal genetic differences on a more appropriate scale than neutral ones such as microsatellite loci. Those analyses may enable us to identify different herring populations, resolve the population structures along the south coast in Norway in a metapopulation context and implement new management strategies.

Even more important for further studies should be the solution of the Landvik mystery. Therefore the origin of Landvik herring and the influence of environmental conditions need to be solved. First of all the original spawning grounds of CSS and Landvik herring must be found, this could be done by continuous and more detailed investigation through scuba diving throughout the spawning season from March until June and additionally use of plankton nets for herring larvae. Secondly new methods should be developed to clearly identify and separate Landvik and CSS herring. This should include genetic differences as well as differences in otolith shape, as demonstrated between Landvik and NSS herring (Lísa A. Libungan, pers. comm.). Thirdly, studies like Folkvord et al. (2009) have conducted, can be repeated between Landvik and CSS herring. Rearing hybrids between those two populations in different environmental conditions may indicate origin of Landvik herring. Therefore similar conditions as found in Landvikvannet and Strandfjorden should be adjusted, also with changing salinity and temperature. Thereby it should be demonstrated if the differences between Landvik and CSS are on genetic or environmental principles. Additionally the acoustic monitoring system can be extended along the coast of eastern Norway, for example each 10 km one receiver unit. With those receiver units herring can be tracked on their migration after spawning in the local area. Moreover, a video inspection of Landvik herring might be useful to estimate the population size. Video cameras might be installed in the narrow part at the canal right after Bufjorden, since during the studies in 2012 the water turbidity was very clear from March until June and all herring should be detected on their migration into the lake. Instead of using video inspection, stationary horizontal and/or vertical hydroacoustic surveys can be conducted in the beginning of Landvikvannet where the first receiver unit (8 Landvikvannet E) is moored (Mann et al., 2008). Horizontal hydroacoustics enable the detection of migrating herring and can study also the surface layer, which cannot be studied by vertical echo-sounding (Boswell et al., 2007; Knudsen and Sægrov, 2002). To use horizontal hydroacoustic the transducers have to be upward facing and bottom-mounted or at least below the oxygen layer in Landvikvannet (Axenrot et al., 2004; Godø and Totland, 1996). Additionally to the acoustic tag we have used, stationary hydroacoustics provide insight into the dynamics and abundance of herring in Landvikvannet. To identify the spawning ground in Landvikvannet and the connected fjords the use of passive acoustics might be a suitable method (Gannon, 2008; Langård et al., 2008; Luczkovich et al., 2008). Beside those stationary acoustic methods more surveys, also during night, with appropriate acoustic equipment can be conducted to trace herring schools inside Landvikvannet.

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6 APPENDIX

A List of abbreviations

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
CSS	Coastal Skagerrak spring spawners
EC	East coast
gonadK	Gonad condition
GSI	Gonadosomatic indix
H_2S	Hydrogensulfide
ILV	Inside Landvikvannet
IMR	Institute of Marine Research
K	Von Bertalanffy growth rate coefficient
L_∞	Asymptotic average length
LV	Landvikvannet
nm	Nautic mile
NNS	Northern North Sea
NSAS	North Sea autumn spawners
NSS	Norwegian spring spawners
O_2	Oxygen
OLV	Outside Landvikvannet
SK	Skagerrak and Kattegat
SNS	Southern North Sea
t_0	Age when the average length was zero
VS	Mean vertebral counts
WBSS	Western Baltic spring spawners
WC	West coast

B Figures

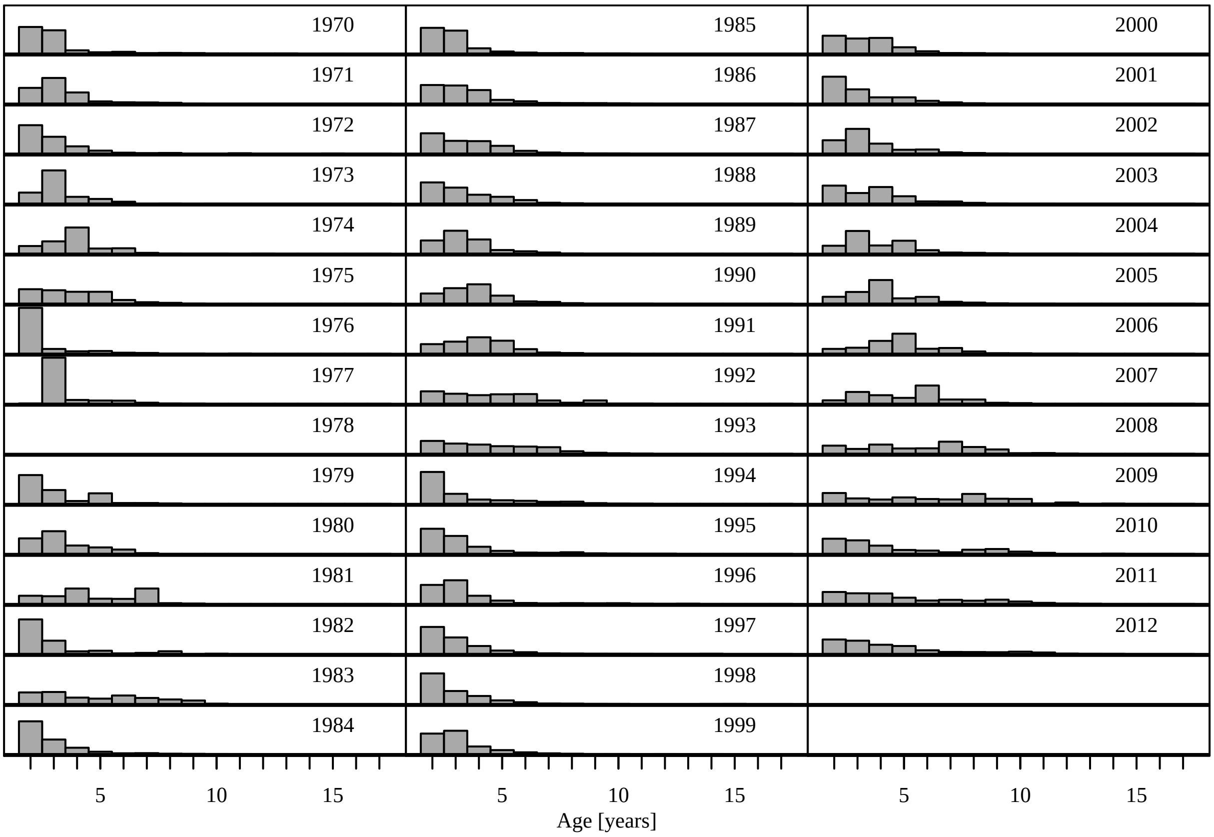

Figure A.1: Annual age distributions from the period 1970–2012 for NNS.

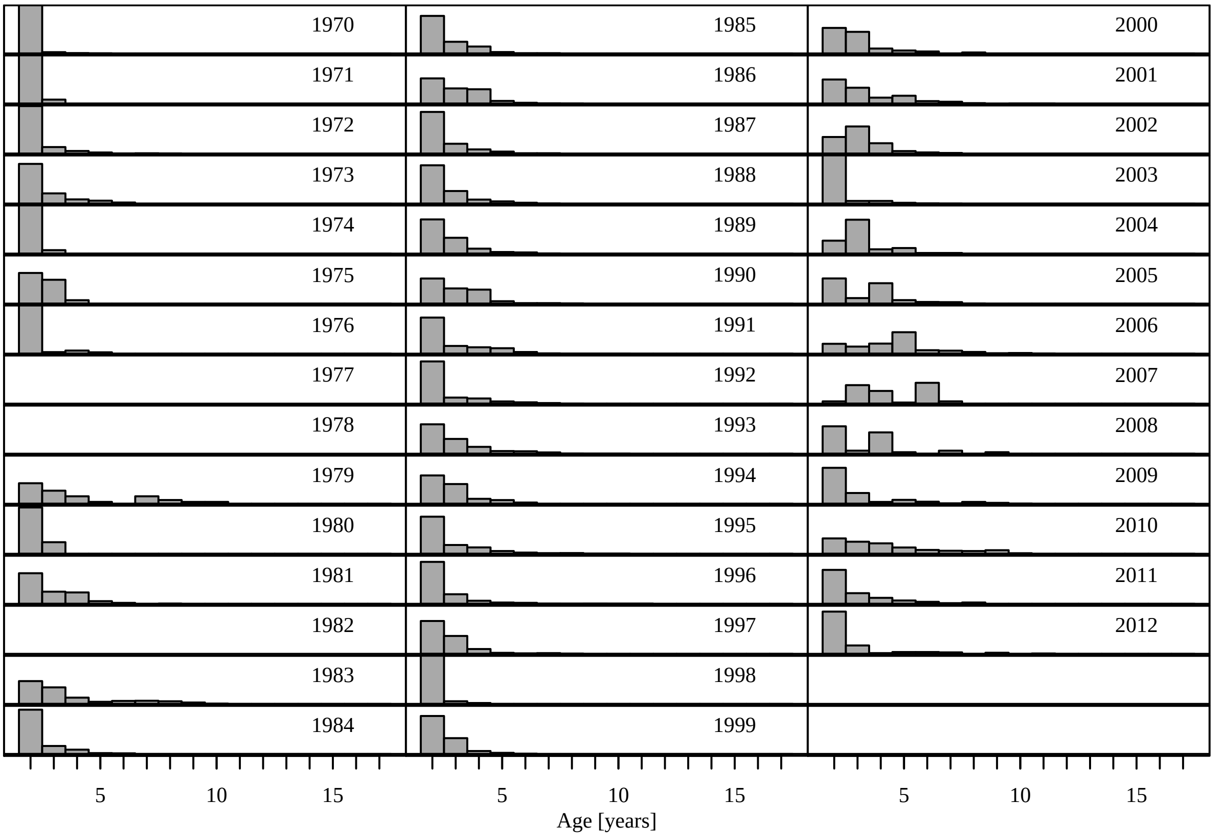

Figure A.2: Annual age distributions from the period 1970–2012 for SNS.

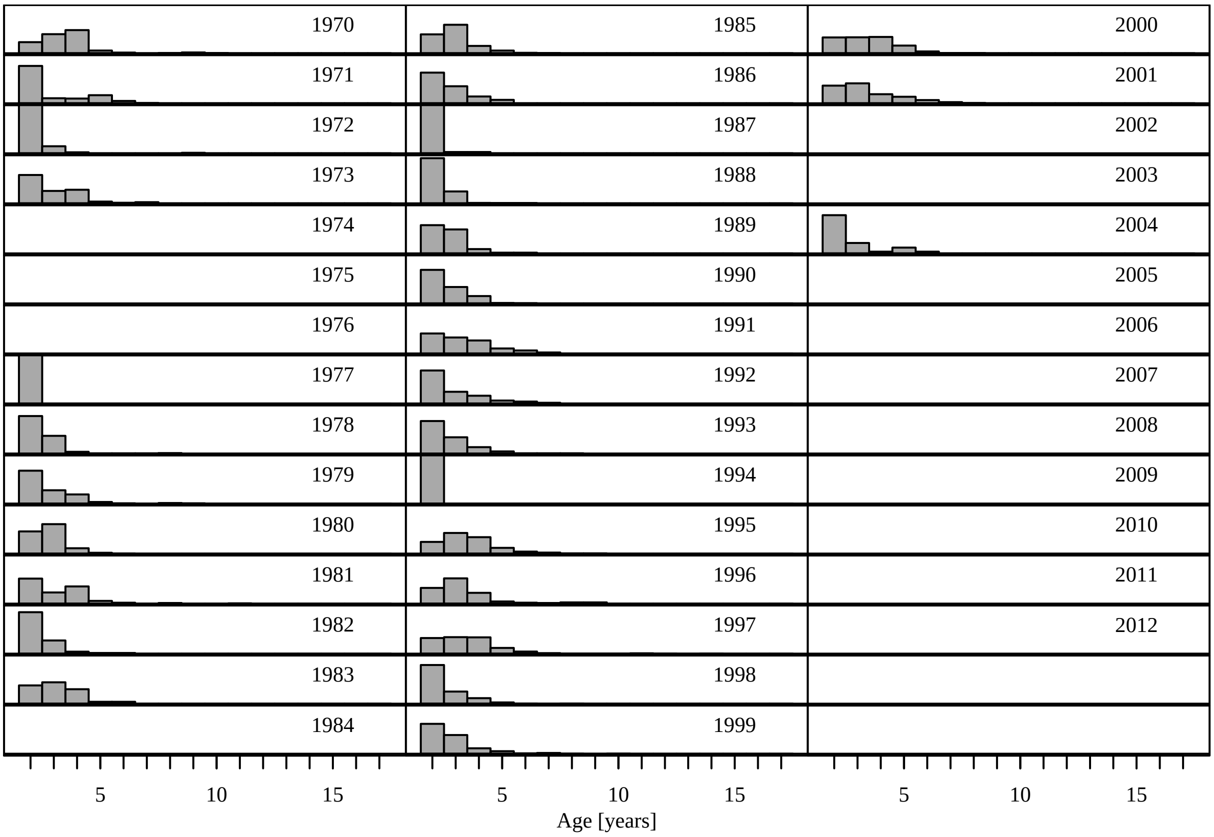

Figure A.3: Annual age distributions from the period 1970–2012 for SK.

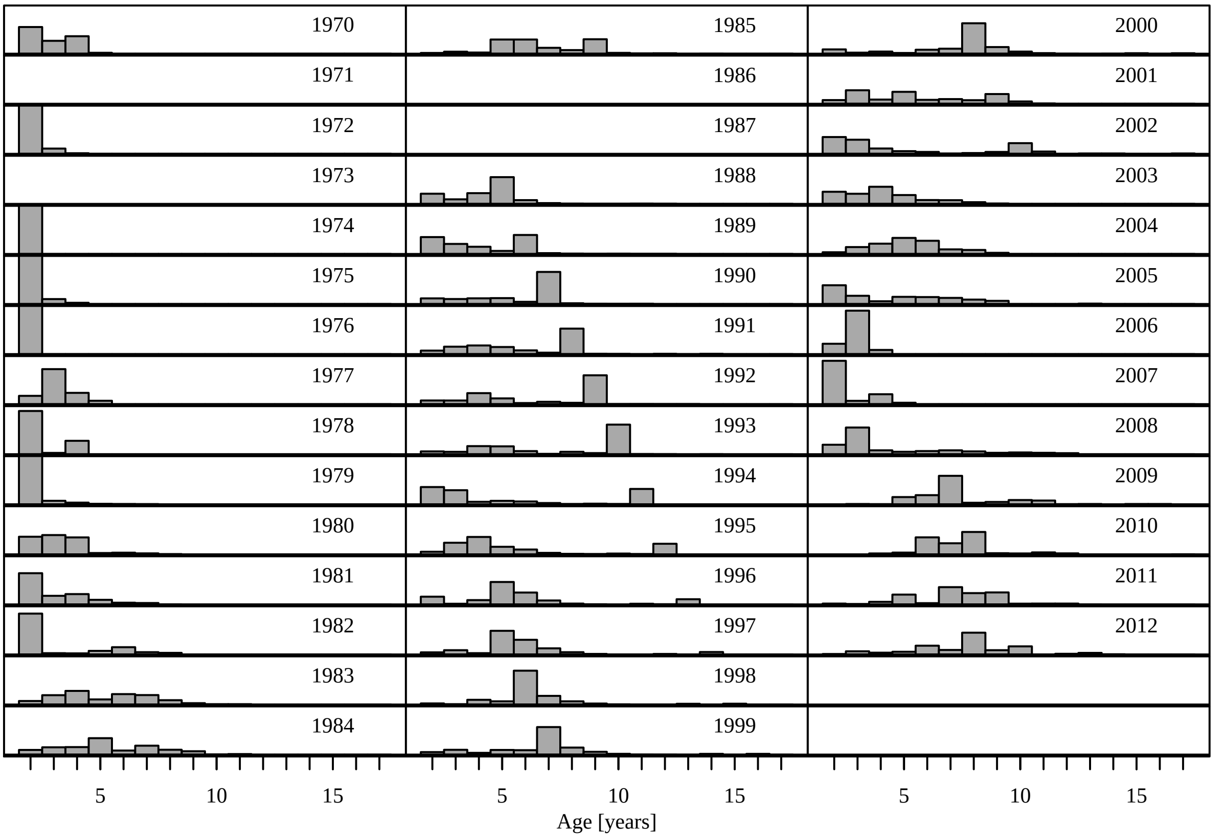

Figure A.4: Annual age distributions from the period 1970–2012 for WC.

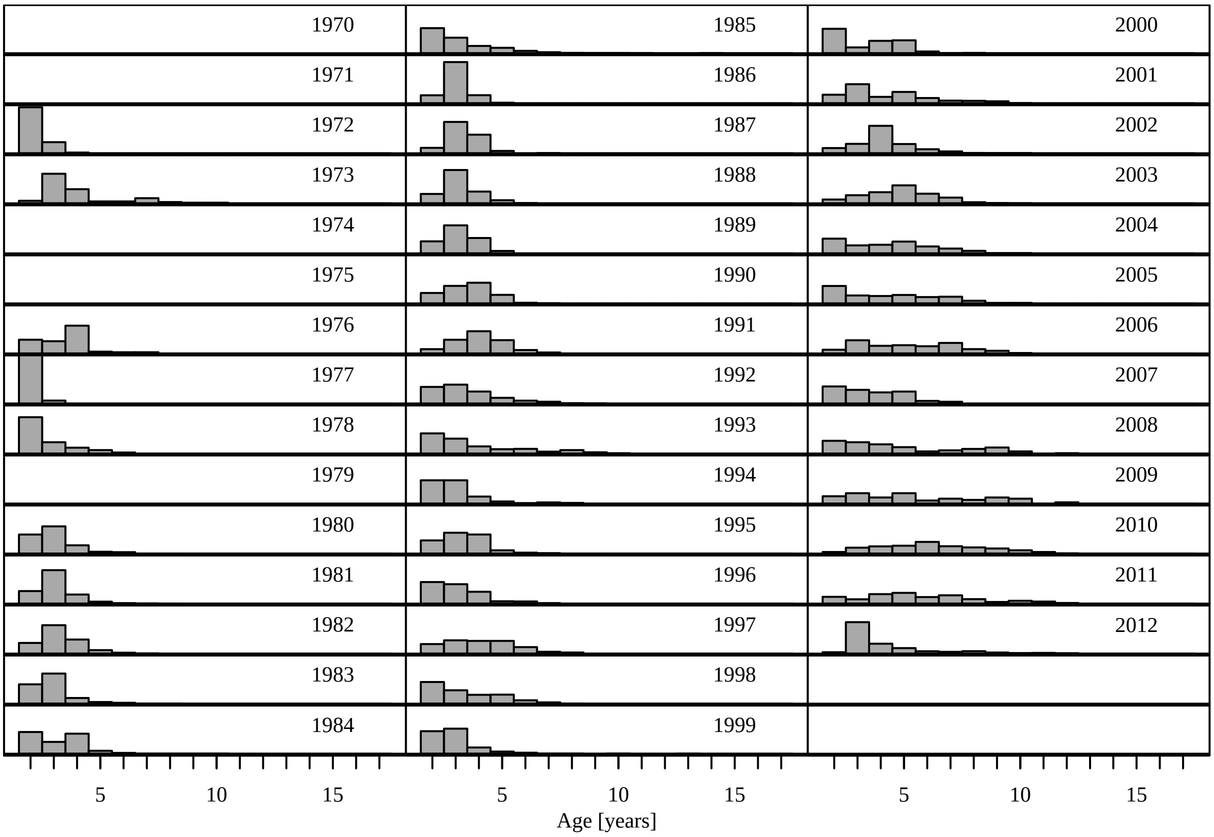

Figure A.5: Annual age distributions from the period 1970–2012 for EC.

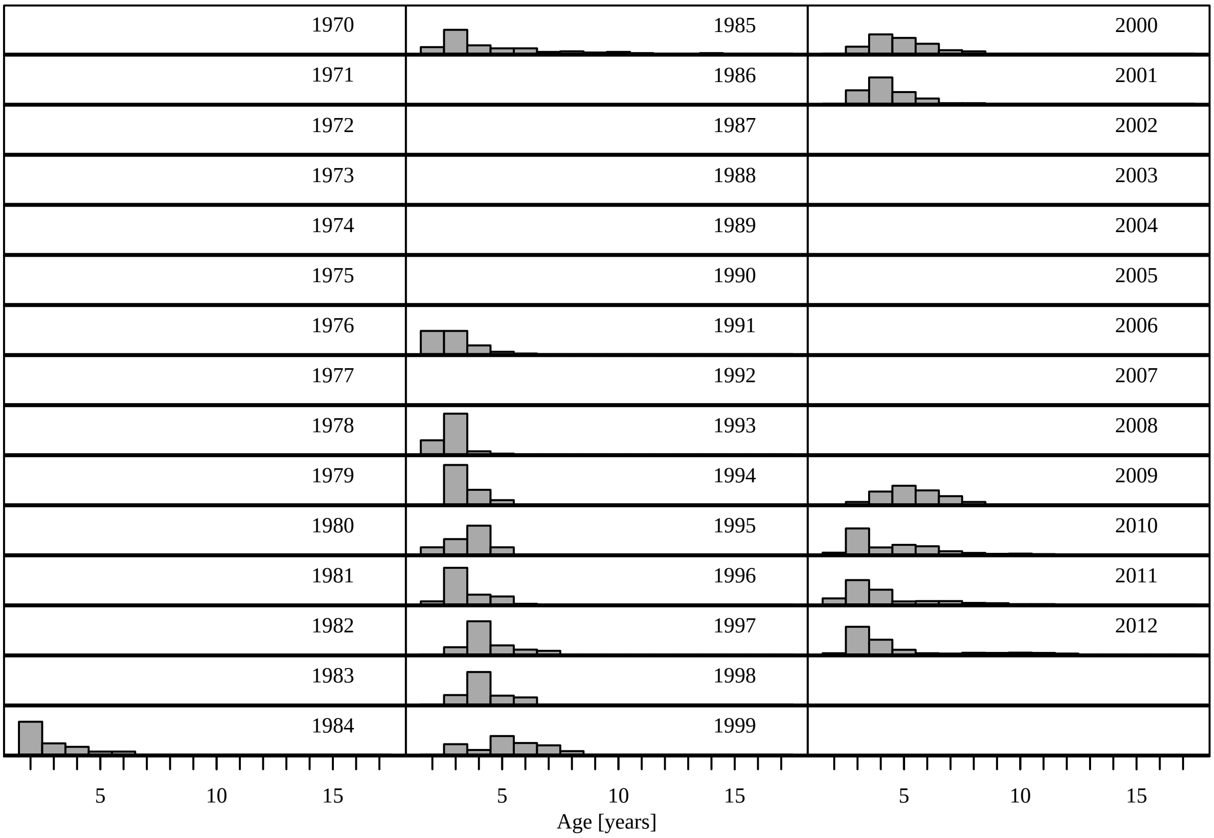

Figure A.6: Annual age distributions from the period 1970–2012 for LV.

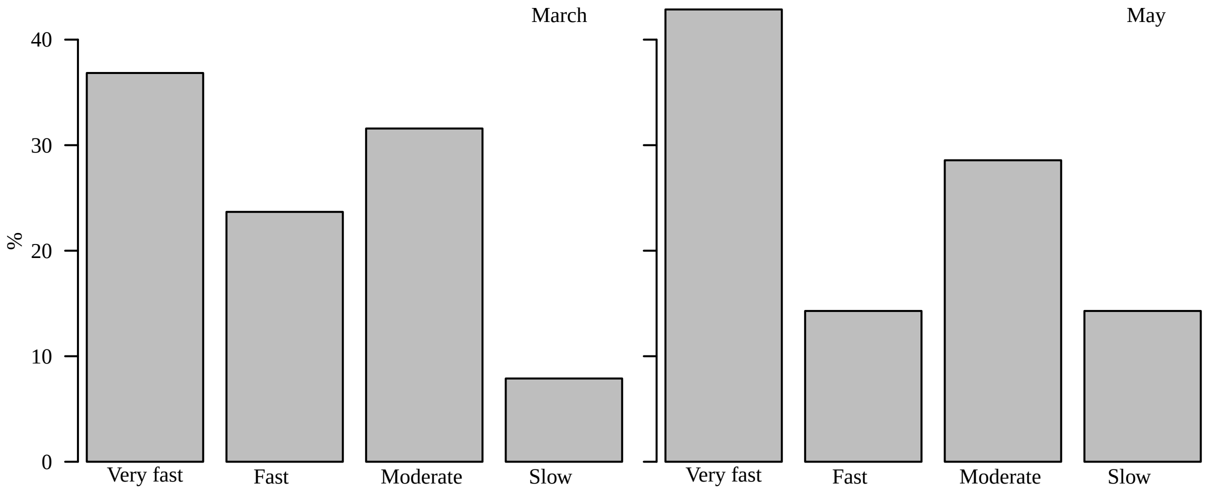

Figure A.7: Herring grouped after their duration within the system for the tagging experiments in March and May. Very fast individuals left the system within the first 10 days; fast left the system between 11 and 20 days; moderate left the system between 40 and 62 days; slow herring stayed longer than 62 days within the system. Herring showing a behavior which defined them as dead were excluded.

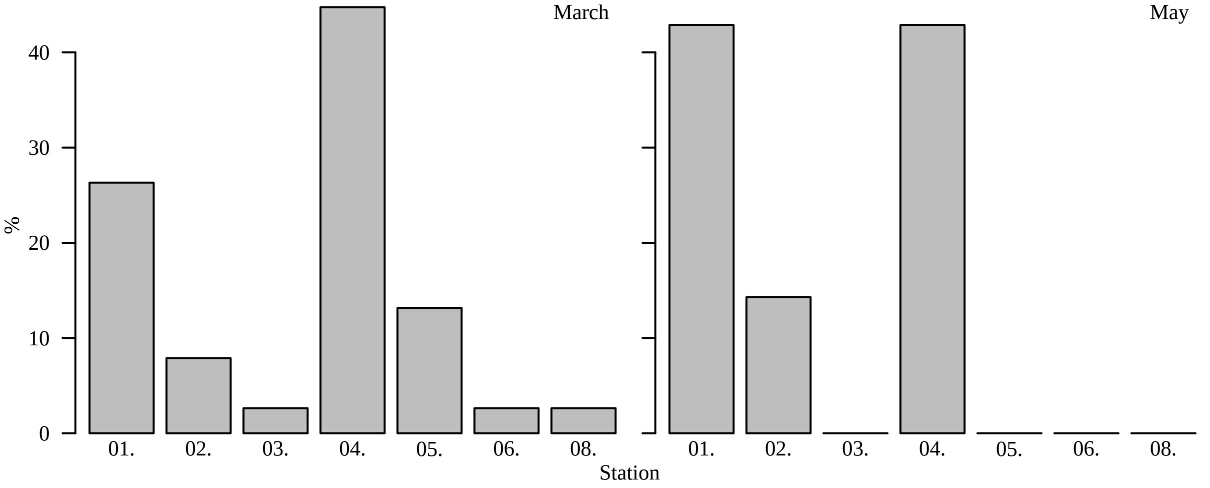

Figure A.8: Distribution of the station of the last detection for the tagging experiments in March and May. Station 06 and 08 are inside the system; Station 01 is the southwards pointed exit; Station 04 the eastwards pointed exit; Station 05 is the last station before entering Bufjorden. Herring showing a behavior which defined them as dead were excluded.

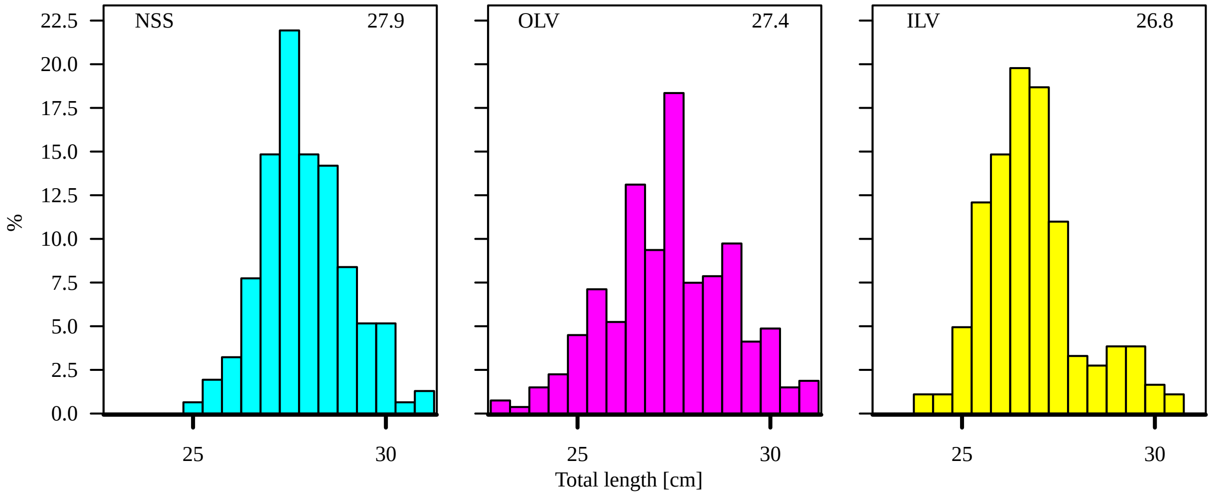

Figure A.9: Length distribution of 3 year old herring typed as NSS, OLV and ILV during the spawning season in 2012.

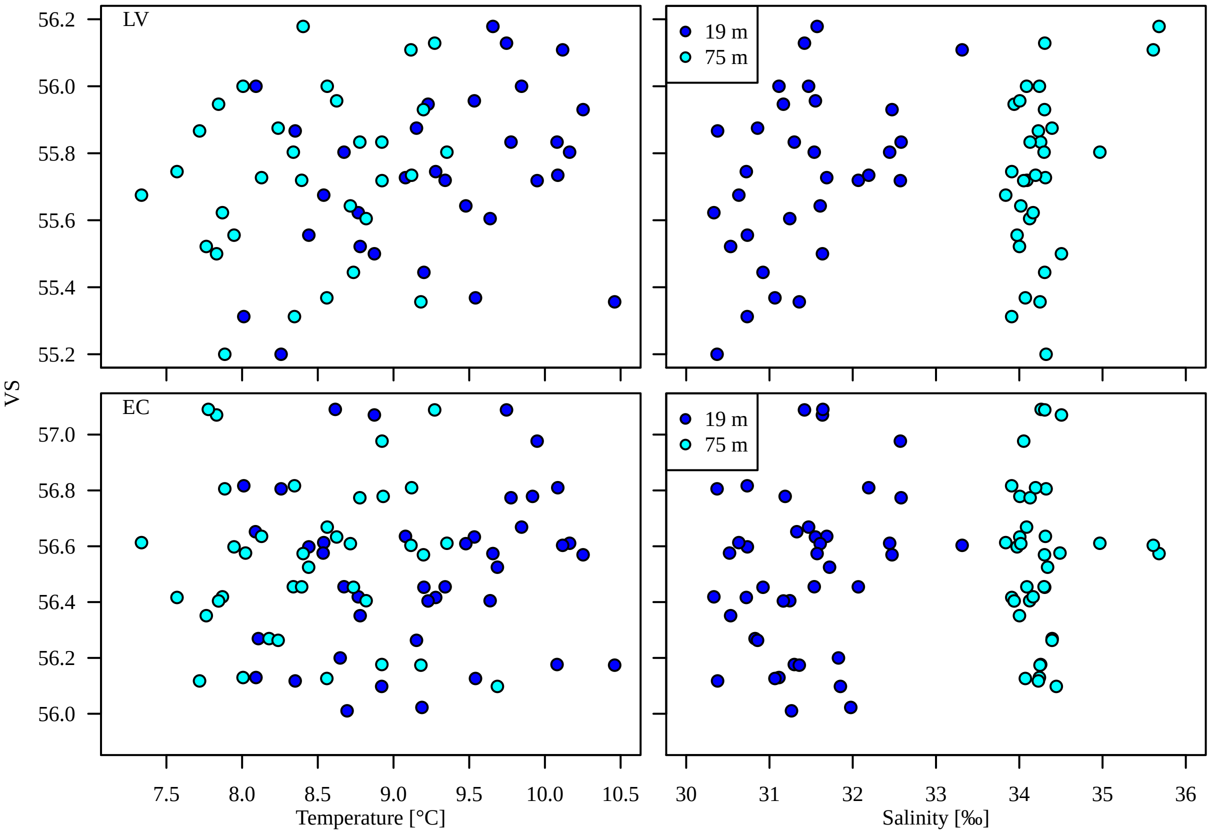

Figure A.10: Correlation between temperature and salinity versus VS for environmental data from Flødevigen.

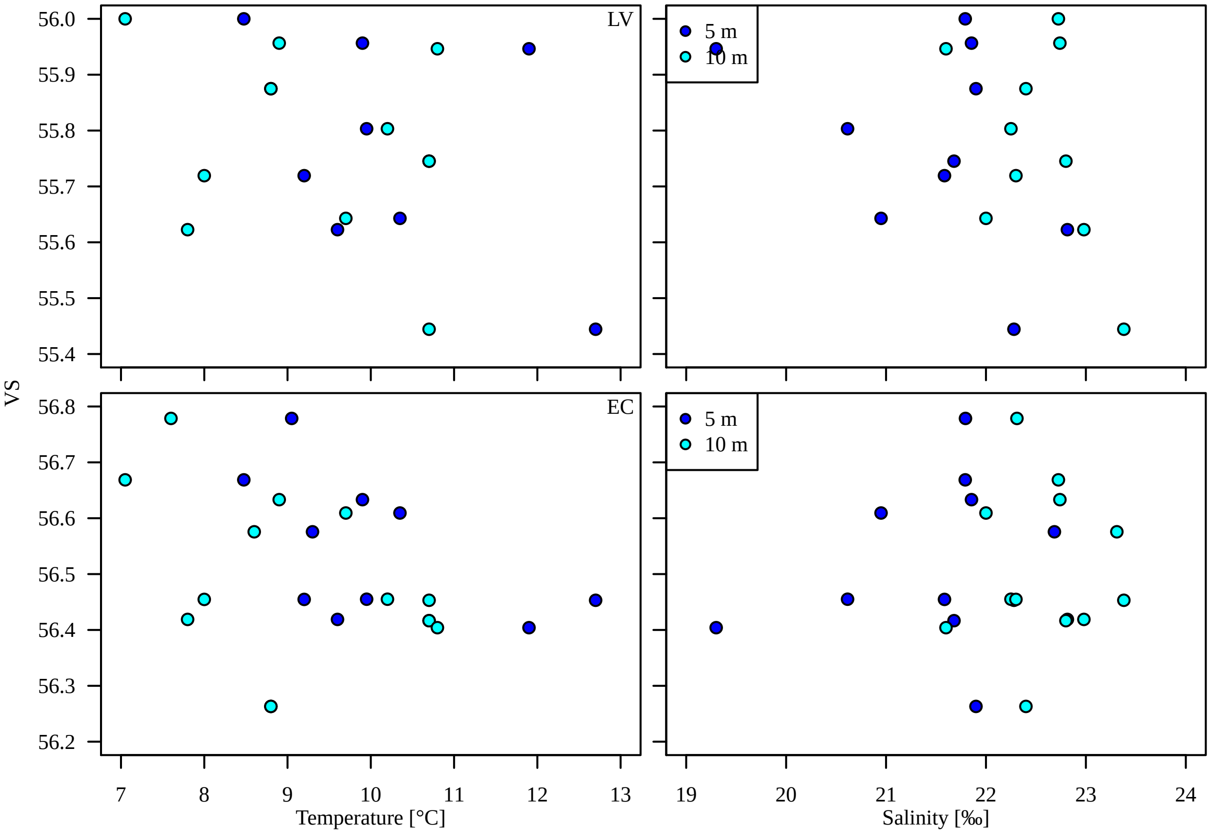

Figure A.11: Correlation between temperature and salinity versus VS for environmental data from Landvikvannet.

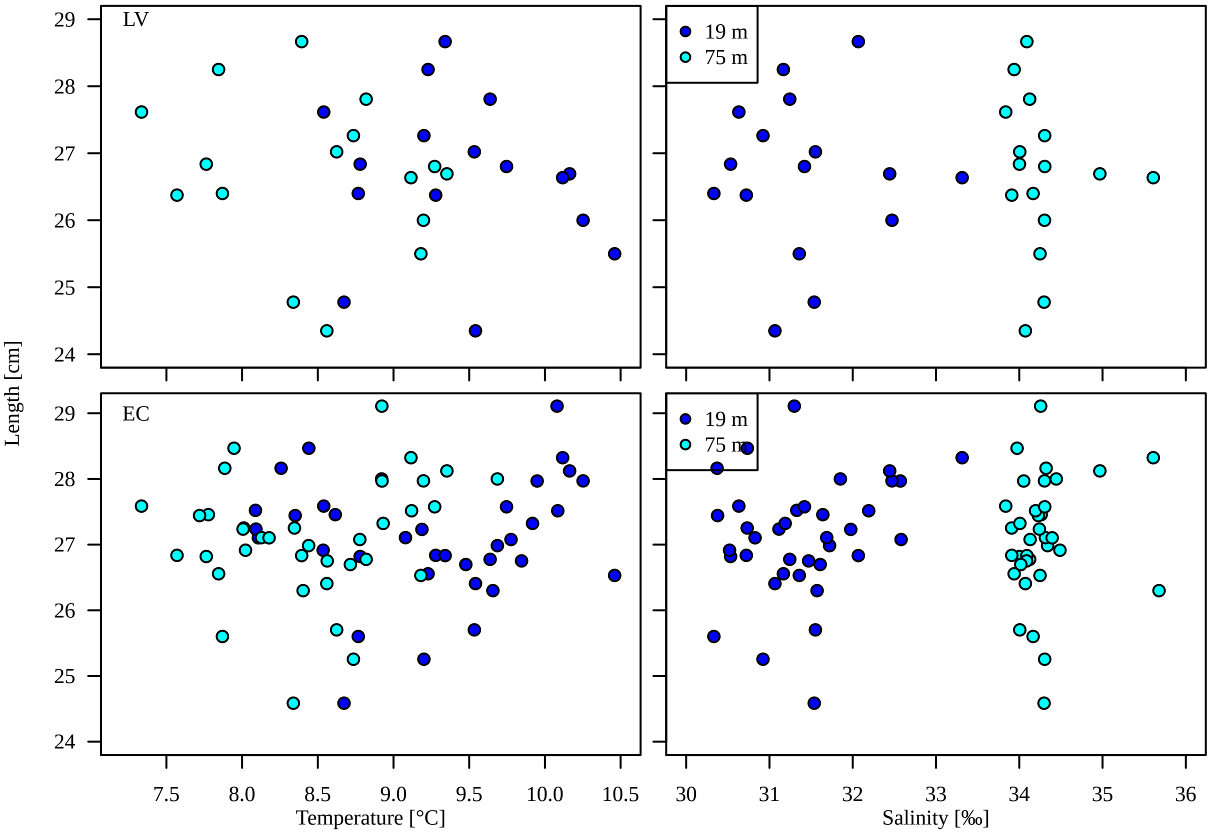

Figure A.12: Correlation between temperature and salinity versus total length of age 3 herring for environmental data from Flødevigen.

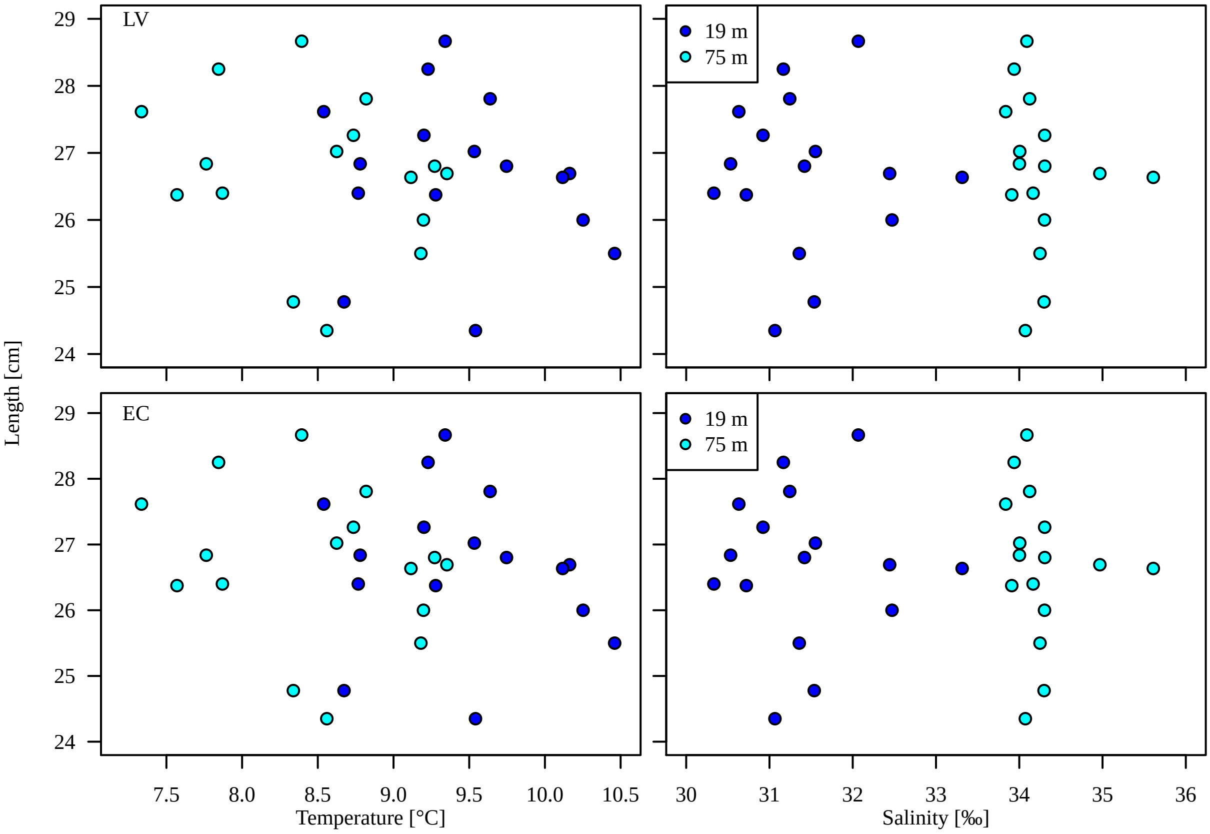

Figure A.13: Correlation between temperature and salinity versus total length of age 3 herring for environmental data from Landvikvannet.

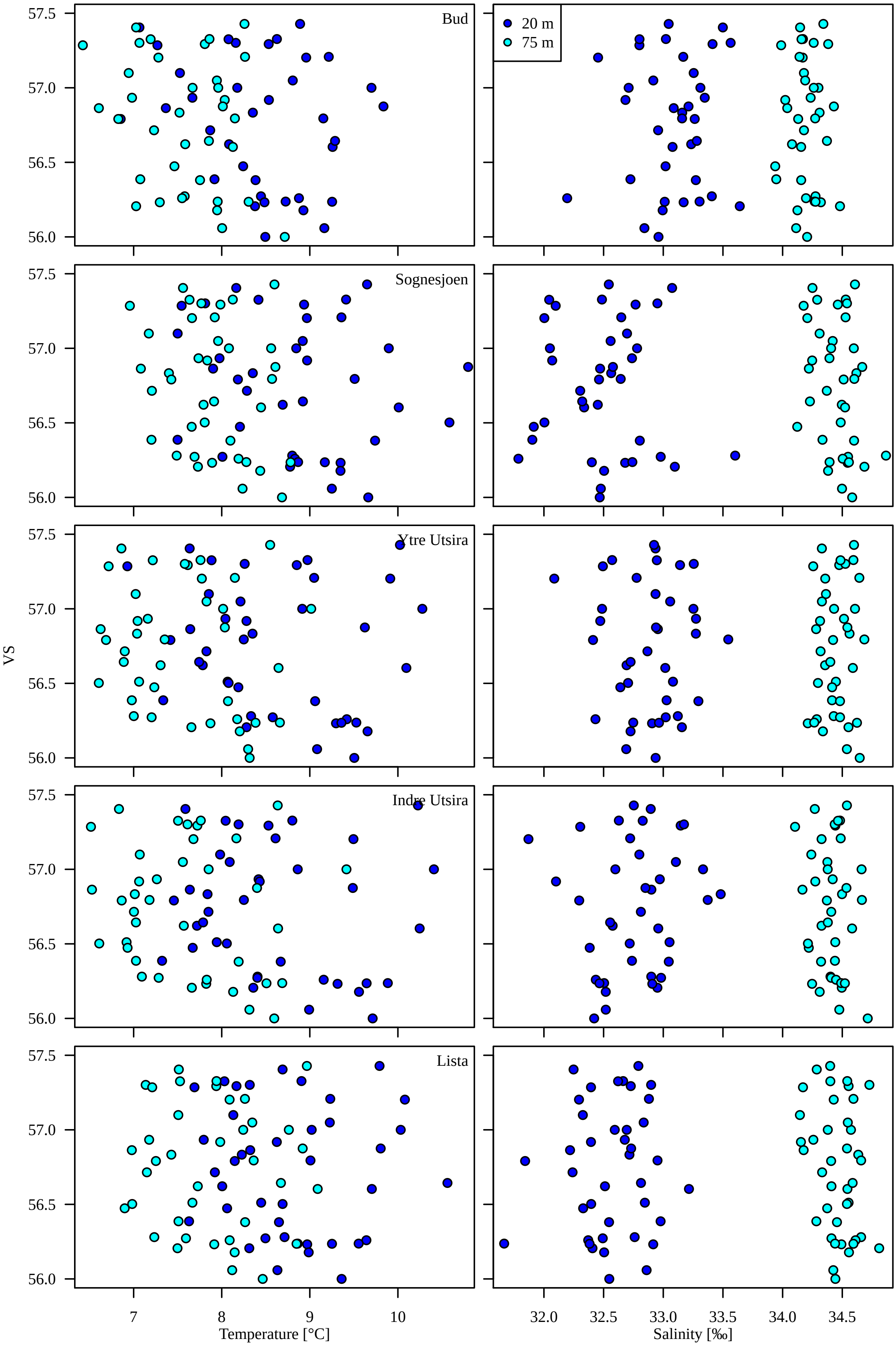

Figure A.14: Correlation between temperature and salinity versus VS of WC herring for environmental data from different stations along the west coast of Norway.

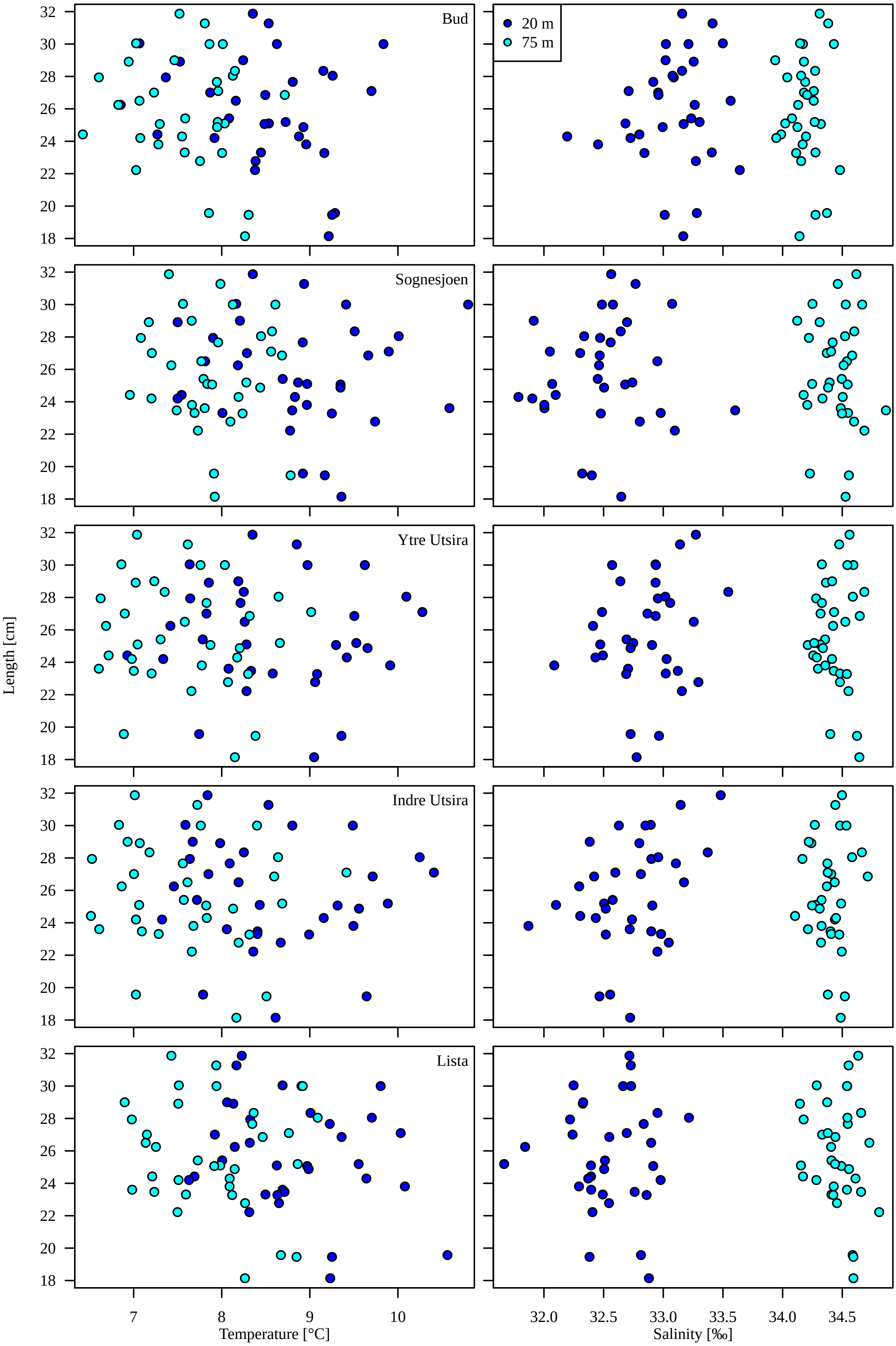

Figure A.15: Correlation between temperature and salinity versus total length of age 3 herring from WC for environmental data from different stations along the west coast of Norway.

C Tables

Table A.1: Live weight kg calculated from landed weight to live weight equivalent for Norwegian spring spawning herring in the statistical area 08 by month and year showing the high abundance of NSS in 2009 and 2010 as registered in the Directorate of Fisheries database as reported 27/5/2013 (* preliminary data).

	Year of catch							
Month	2005	2006	2007	2008	2009	2010	2011	2012*
1					58			
2	21160				171922	3302863	609128	897324
3	24525	32596	16514		19051966	14876991	6528433	6283215
4	129197	650	980	4840	2301219	1000318	52000	13388
8	1000							
9					851			
10			100					
11		72 808				450		
12	200							
Total	**176082**	**106054**	**17594**	**4840**	**21526016**	**19180622**	**7189561**	**7193927**