MASTER OF SCIENCE IN FISHERIES BIOLOGY AND MANAGEMENT

Strategies for partition between reproductive investment and body growth in stationary and migratory stocks of Atlantic herring

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Abstract

The present study focused on the trade-off between reproductive investment and body growth of migratory and stationary Atlantic herring (*Clupea harengus*) populations. Published data from Norwegian spring-spawning (NSS) herring, a highly migratory stock caught on the spawning grounds off the Norwegian coast, was compared with two local/stationary herring populations that spend most of their life cycle relatively isolated in semi enclosed bays (Lindåspollene and Trondheimsfjord). One third sample was also taken in Landvikvannet (southern Norway) but so far very little is known about this herring population. In Lindåspollene sampling was carried out between late January and March 2009 and 2010 and in Trondheimsfjord only one sample was taken in March 2010. The sampling in Landvikvannet was carried out in May 2010. Inside Lindåspollene two groups of herring were differentiated by otolith pattern and by bimodal age frequencies. The study compared fish condition (*K*), gonadosomatic index, female fecundity and body growth between these populations just before spawning. NSS herring had the highest growth rate compared to all other groups but it was also one of the groups with higher value of *K* while Trondheim the lowest. Migratory NSS herring presented the lowest relative fecundity together with one of the samples caught in an outside area of Lindåspollene. Overall, results from relative fecundity seem to indicate the existence of a threshold value of about 270 oocytes per gram of fish that separates the migratory populations from the stationary ones. Energy must then The present results support the findings of Atlantic herring exhibiting a large dynamic range of reproductive strategies which are in turn a reflection of population adaptations to their environment. However, to fully evaluate the whole range in reproductive tactics, the relationship between the number and the size of the eggs should be further studied.

Key words: energy, trade off, reproduction, growth, life history, herring

1 Introduction

Considerable attention has focused on the quantitative patterns present in fundamental life history parameters of marine fishes (Kawasaki, 1980; McCann and Shuter, 1997; Rochet, 2000; Roff, 1984; Winemiller and Rose, 1992). In a natural environment, fish have limited energetic resources so a direct trade-off should exist between body growth and reproduction. This is considered the principal assumption in life history theory (Roff, 1983; Stearns, 1992).

Fishes exhibit a vast diversity of reproductive strategies and associated traits such as type of spawning, mating system, spawning sites and season, fecundity (determinate versus indeterminate), etc (Murua and Saborido-Rey, 2003). The different strategies reflect population specific life history adaptations to the surrounding environment and are related to their requirements for survival (Cole, 1954).

Within the same species, sub-populations often occupy a wide range of different habitats and some of these listed traits may vary, i.e. manifestation of different life history tactics. Intraspecific variances in life history characteristics have been shown for several fish species, e.g. American shad *Alosa sapidissima* (Leggett and Carscadden, 1978), Atlantic herring *Clupea harengus* (Jennings and Beverton, 1991), European plaice *Pleuronectes platessa* (Nash et al., 2000) and Atlantic cod *Gadus morhua* (Thorsen et al., 2010). Such studies have shown to provide valuable information of how the life histories are formed.

The principal objective of a reproductive strategy is to produce the largest possible number of offspring and ensure that those are in turn able to produce a new generation (Kjesbu and Witthames, 2007). However environment is usually unstable and food is not always available. Thus, there must be an underlying strategy for fish to allocate the available energy in order to maximize reproductive success. To handle such variations several mechanisms are known to exist allowing fish to alter their reproductive investment. Fecundity regulation by selective resorption of vitellogenic oocytes (atresia) has been reported in repeat spawners of Norwegian spring-spawning (NSS) herring (Kurita et al., 2003). Also, it has been observed changes in the duration of the spawning migration (Slotte, 1999b) or even completely missing a reproductive event by total reabsorption of developing oocytes (Rideout et al., 2005).

Since life theory strategies are the primary features for population reactions to environmental changes they can be used to classify standard population responses (King and McFarlane, 2003). It is therefore of great importance to obtain such information as part of studies on population stability and formation of year-class strength. For instance, Nash and Dickey-Collas (2005) have shown that for North Sea herring some stages of the life history can influence population recruitment.

Two species of herring are currently recognized: Atlantic herring and Pacific herring (*Clupea pallasi*), still different stock units are found within these species (Whitehead, 1985). In this study we focus on the Atlantic herring. More specifically, the NSS herring, a highly migratory species which is one of the largest and most important single fish stock unit in the North Atlantic (Dragesund et al., 1997). It is also known as the largest herring stock in the world (Toresen and Østvedt, 2000) and one of Norway's most important fishing resources. During centuries, this valuable stock has shown great fluctuations in abundance, being the most dramatic period when the stock collapsed to the state of nearly extinction in the late 1960's (Dragesund et al., 1997). However, with successful management, the individual growth rates increased in the years following the collapse and at present, the stock is considered fully recovered (Toresen and Østvedt, 2000).

In recent years, NSS herring covers a large part of the Norwegian Sea during the feeding period (April-August), while spending the wintering period (September-January) in the Lofoten area, northern Norway (Dragesund et al., 1997). In mid-January the stock starts migrating to a wide range of spawning grounds that are from close to the wintering area (69º N) in the north to Lista (58º N) in the south, ranging circa 1500 km (Johannessen et al., 1995).

NSS herring is a suitable candidate of the study of reproduction investment as it does not feed for about half a year during the wintering and the spawning season (Slotte, 1999a). Thus, herring must allocate energy to gonad development and spawning migration from energy resources stored during the feeding period in the Norwegian Sea. This eliminates any influence that unaccounted feeding activity can have on fecundity. Also, the long migration from the wintering area towards southern spawning grounds along the coast is specially demanding; Slotte (1999) estimated the whole body energy loss (in kJ) to increase 3-4 times compared to the wintering period.

To estimate fecundity one must give special attention to the different spawning styles that different species of fish present. Herring is a determinate spawner which means that there is no recruitment of new oocytes into vitellogenesis during spawning, which makes it possible to estimate fecundity directly by counting the number of vitellogenic oocytes existing before spawning occurs (Kjesbu 2009).

Reproduction requires energy, not only for sex cell production but also the associated physiological behavior. The energy allocation by females to reproduction includes also a trade-off between egg number (fecundity) and size (Roff, 1992; Stearns, 1992). Still, the assessment of fish fecundity may be use as a proxy to determine female reproductive investment.

Moreover, herring population dynamics are rather complex and are known to have different reproduction patterns, spawning seasons (Spring/Autumn) and spawning areas (Husebø et al., 2005). In Norway, a general division is made between coast or fjords stocks and ocean stocks. Along the Norwegian coast there are a number of small fjords and semi enclosed bays in which small, more or less self contained herring populations live. Few of these populations have ever been studied, the ones that have, usually take the name of the general area or fjord (Holst et al., 2004). These local herring usually have specific growth characteristics that distinguish them from the oceanic herring (Lie et al., 1978).

In this study we focus particularly on four different populations of Atlantic herring, i.e., two acknowledged local, stationary and more or less self contained herring populations (Lindåspollene and Trondheimsfjorden), a more southern (Landvikvannet) but less well-studied population and the oceanic NSS herring stock.

Lindåspollene where a small local population of herring lives is a semi-enclosed marine system connected with the outer sea via a narrow sill. However, recent studies (Johannessen et al., 2009) have shown that more than one herring component is found in this area during the pre- and spawning period.

Landvikvannet used to be a fresh water lake but in 1980 a canal (3 km long) was built connecting this lake to the sea. Consequently, the water level was lowered at sea level and salt water got into the lake, particularly in high tides. No literature was found on the biology of the Landvikvannet herring and the origin of this group of fish is, so far,

unknown. However, similar vertebrae counts between this population and the Baltic herring suggest a relationship between these two populations (Slotte 2011, pers. comm.). No larvae were found after the spawning period inside this lake so there is no evidence that they actually spawn in this location (Slotte 2011, pers. comm.). This study seems to be the first to investigate this population reproductive characteristics.

The final objective of this study is to assess how the energetic investment into egg production and body growth is allocated between stationary and migratory herring populations. With this analysis I aim for a better understanding of the underlying factors conditioning this species reproductive strategy and dynamics.

2 Material and Methods

2.1 Location of the samples

For this study, samples were taken at different locations on the Norwegian coast (Figure 1). Data of the oceanic Norwegian spring spawning (NSS) herring stock caught in the Norwegian Sea in February 2010 was consulted from the Institute of Marine Research (IMR) database (Table 1).

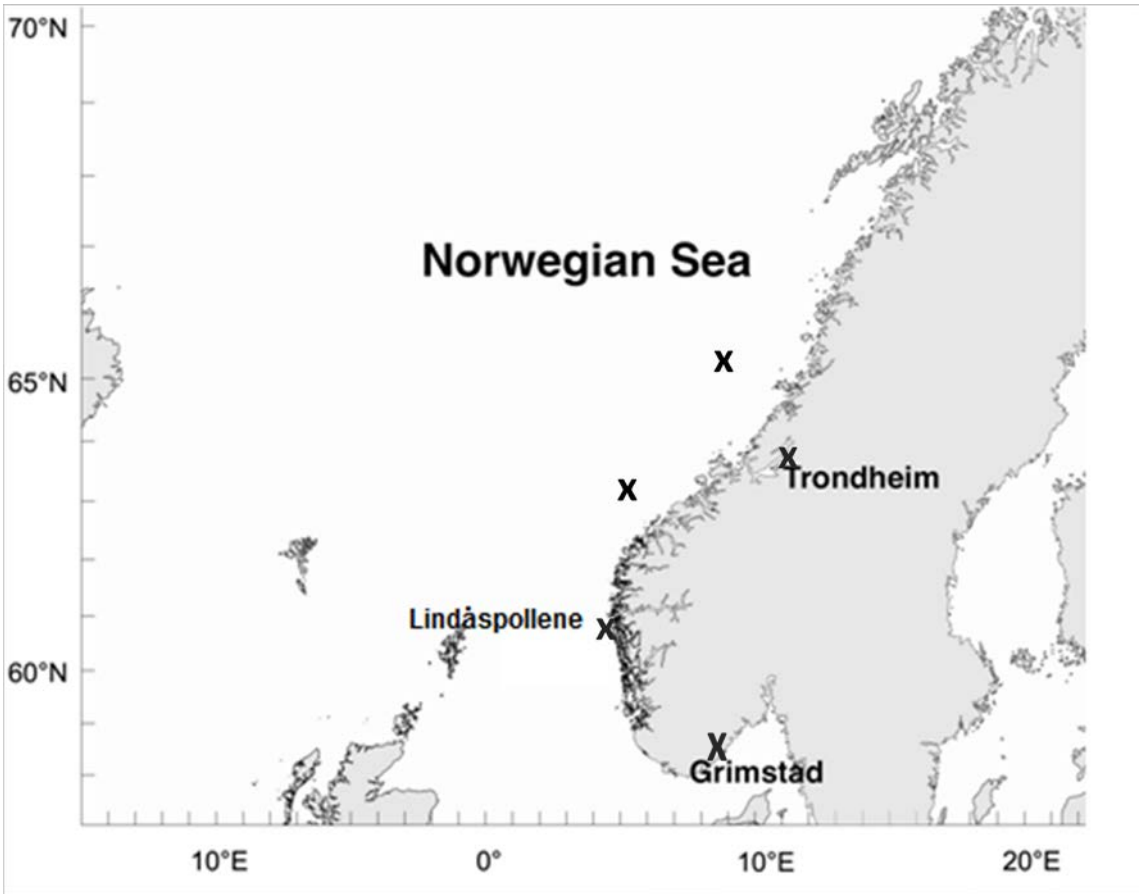

Figure 1. Map showing the location of the sampling sites.

Lindåspollene is a well-defined marine ecosystem (Figure 2) located approximately 36 km north of Bergen (West of Norway) where a small population of local herring lives. The local herring from Lindåspollene (LP) has a slower growth rate, lower mean number of vertebrae and smaller size-at-age than the NSS herring (Lie et al., 1978).

Several samples were taken between late January and March during the spawning seasons of 2009 and 2010.

In 2009, one sample was obtained from an outside area of Lindåspollene, closer to the Lurefjord while the other samples were taken inside the bay. According to Johannessen et al. (2009), a higher contribution of strange herring (most likely NSS herring) is expected to occur outside Lindåspollene. Therefore the NSS individuals caught outside the bay (NSSOLP) were analysed separately from the NSS herring caught inside the bay (NSSILP). All together, a total of 250 females were sampled and 234 of these were classified to stock by otolith analyzes. Of these, 89 individuals (38%) were identified as local LP herring while the rest were classified as NSS herring. Most of the NSS herring were caught outside the Lindåspollene sill where only two LP females were found.

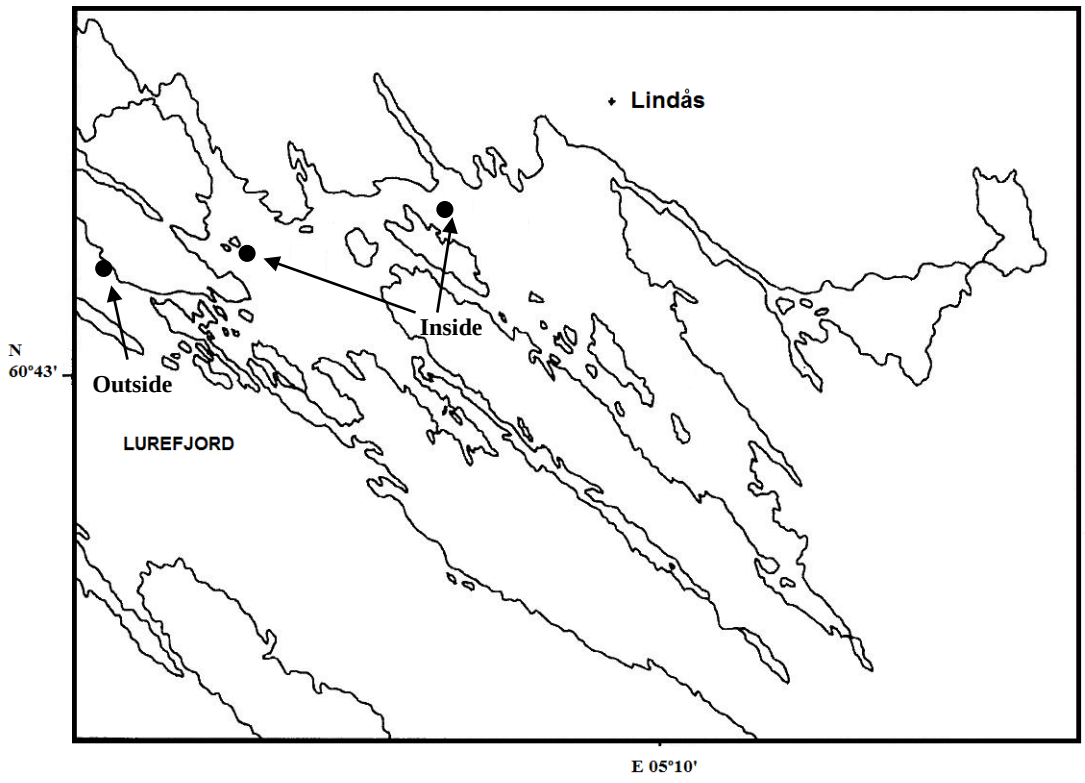

Figure 2. Map of Lindåspollene, main location of the samples is marked with dark circles.

In 2010 all samples in Lindåspollene were taken only inside the bay, thus the fish were categorized in just two components (NSSILP and LP). In total, 106 females were sampled and 99 were stock classified by otolith analyzes. Approximately 79% of the females were LP herring and the rest NSSILP.

In both years the samples were taken using monofilament gillnets (26-34 mm mesh size). After capture, the herring were sampled immediately or kept intact on ice and taken to the laboratory in Bergen where they were sampled still fresh within maximum 24 hours.

In March 2010, a total of 131 individuals were caught with gill nets by a local fisherman from a local herring population in Trondheimsfjorden (near Trondheim). The fish were kept unopened in a cold room until being worked up the next day. Each fish was stock identified by otolith analysis and the majority of the sample was classified as local Trondheim (TR) herring. Only 8 individuals were classified as NSS herring which were excluded from the analysis. In this study the information of 59 prespawning TR female herring is presented.

In May 2010, 223 herring were collected from Landvikvannet – near Grimstad (south of Norway). Overall, very little is known about this herring. For the purposes of this study only, the group was named Landvik herring (LV). In total 106 females were sampled.

2.2 Length, weight, age and gonad samples

For all stocks, individual total length (*TL*) was measured to the nearest 0.5 cm (but presented in mm in spreadsheets) below and whole body weight (*W*) was recorded to the nearest gram. In all individuals the gonads were carefully dissected and weighed fresh (W_g) to the nearest gram. For each female one sub-sample of ovarian material was collected from the right lobe and immediately fixed in 3.6 % phosphate-buffered formaldehyde in a plastic vial and stored for at least 14 days before any analysis. Otoliths were collected from almost all individuals and age and stock determination was read by experienced age readers.

Information about length, weight and age from oceanic NSS herring was obtained from the IMR central database (CDB) for February 2010. Fecundity was then estimated using the fecundity-length-Fulton's condition (*F-LK*) relationship for NSS herring previously established for the spawning season of 2008 with $r^2 = 0.78$ (Kennedy et al., 2011).

Eight maturity stages (Mjanger et al., 2007) were discriminated based on visual inspection of the gonads: 1, immature; 2-5, maturing or prespawning; 6, spawning; 7, spent; and 8, resting stage.

Many fish caught in Landvikvannet were showing early signs of start of spawning (i.e. hydrated/ovulated oocytes). Thus the gonadosomatic index (GSI) was compared between the females in maturity stages 5 and 6; the GSI is normally a function of maturity stage. The stage 6 group showed a significant lower value of GSI (T-test; $P < 0.001$) compared to stage 5 meaning that the stage 6 females likely had already lost some eggs. Consequently all females in stage 6, together with any immature or spent fish (maturity stage 1 or 7) were excluded from the present analysis.

2.3 Historical length-at-age data

Due to the lack or low amount of sampled data in many age-groups from the studied populations, historical length-at-age data were gathered to establish the growth curves of each population. The following information was used: data from Landvik herring caught during 1984-1985, 1991, 1993-2001 and 2009-2010 from April to June (spawning season); from Trondheim collected during 1976-2008 from October to December (wintering/end of feeding season) and oceanic NSS herring collected from 1970 to 2010 from January to March were all taken from the IMR CDB. Published data from Lindåspollene herring caught from 2005 to 2007 (from January to April) were also consulted (Johannessen et al., 2009).

Table 1. Number of fish sampled and analysed in each area and period of time. *Individuals classified as NSS herring caught inside Lindåspollene; ** Estimated fecundity.

Sampling period	Geographical area	Stock	No.		No. of females analysed	
			♀	♂	Fecundity	Atresia
Local/stationary						
Jan.-Mar. 2009	Lindåspollene	LP	89	79	54	17
Feb.-Mar. 2010	Lindåspollene	LP	78	58	69	15
11th Mar. 2010	Trondheim	TR	64	67	60	10
Oceanic/Migratory						
Feb. 2010	Norwegian Sea	NSS	153	148	134**	-
Other						
Jan.-Mar. 2009	Outside Lindåspollene	NSSOLP	85	55	84	9
Jan.-Mar. 2009	Lindåspollene*	NSSILP	57	42	45	7
Feb.-Mar. 2010	Lindåspollene*	NSSILP	21	14	21	3
12th May 2010	Landvikvannet	LV	106	117	57	4
Total			653	580	524	65

2.4 Fecundity samples

All samples were analyzed for fecundity using the auto-diametric method (Thorsen and Kjesbu, 2001) which is a rapid method for estimating oocyte density (number of vitellogenic oocytes per gram of ovary tissue) using an image analysis system. With this method, fecundity estimation is based on diameter measurement rather than counting.

Only a portion of each sample was used for automatic oocyte measurements which was discarded after used in the image analysis, the remaining part was saved and later embedded for histological analysis. A Pasteur pipette was used to loosen apart the oocytes and connective tissue. Buffered formaldehyde was added to fill the surface of a Petri dish and a drop of dishwashing soap (Zalo) was added to reduce the surface tension which facilitated all oocytes sinking to the bottom.

All measurements were performed using the free program ImageJ 1.42e (available at http://rsb.info.nih.gov/ij) on a Mac OSX version 10.5.6 connected to a digital camera (Qimaging micropublisher 5.0 RTV) on a stereo microscope (Olympus SZX12 with a SZX-ILLB200 light foot). The image capture program QCapture was used to control all camera functions and some advanced functions, such as binning and region of interest (ROI). Both microscope and camera were turned on so that the temperature was stable (30 min) before any analysis starts. The microscope magnification was set at 7×. The pictures were set at binning 2. In order to automate the measuring procedure and data handling, specific macros were used previously developed in ImageJ and Excel.

In ImageJ, a macro based on roundness factor thresholding was run so that only particles with roundness factor in the range of 0.85 – 1.0 were counted. In general, discarded particles were shown to be connective tissue, damage oocytes or clumps of oocytes. To each measured particle was given an identification number in the order it was measured.

For each oocyte, the following variables were measured: area, perimeter (length of the line drawn around the particle), ellipse major and minor axis and circularity. A minimum of 200 oocytes was analyzed per sample and the oocyte diameter was automatically obtained for each oocyte. The results were then copied to a Microsoft Excel 2011 spread-sheet with pre-arranged basic statistic formulas. From the oocyte frequency distribution, mean, standard deviation, max, min, and 95% confidence

interval (95% CI) of the mean oocyte diameter were automatically calculated. The mean diameter of the leading cohort (LC) was defined as the average diameter of the largest 10% measured oocytes. The mean diameter of the LC refers to the largest oocytes that are likely to mature and ovulate first. It is thereby used to estimate the time to start spawning (Kjesbu, 1994).

2.5 Atresia

Only a pre-screening process was performed to examine the level of atresia. For the samples caught in Trondheim and Landvikvannet, 10 gonads were selected from each location for histological analysis. However, for the samples from Lindåspollene (2009), a total of 43 gonads were selected because more samples were also taken during that year in that location. In 2010, 20 samples from Lindåspollene were screened for atresia. The selection of the samples was made randomly but before the results from the otolith analysis was finished. Thus, the final total number of analysed samples from each herring population varied. The selected samples (preserved in 3.6% buffered formaldehyde) were dehydrated in ethanol in progressive series up to 95% and embedded in Technovit® 7100 (based on methacrylate) following a standard histological protocol. The diameter of the LC of the oocytes from each sample was checked in the image analysis data and used as the distance between sections so that the same oocyte was not counted twice. All sections (4μm thick) were stained with 2% toluidine blue and 1% tetraborate, dried and mounted on microscopic slides using Mountex. This process stains the cell nucleus, the yolk granules and the chorion in different degrees of blue.

Each section was analysed under the microscope and the total number of normal and atretic oocytes were counted. For each gonad sample, a total of 100-150 oocytes were counted from one, sometimes two sections. The classification of Hunter and Macewicz (1985) discriminates different types of atresia. However, for a more precise classification, only the α stage was considered (Figure 3).

The relative intensity, i.e. percentage of oocytes that were atretic (100 × number of atretic oocytes/(number of normal and atretic oocytes)) was calculated. However, atretic oocytes are less likely to be sectioned as they are smaller than normal oocytes.

Therefore the relative intensity of atresia was adjusted using the equation from González-Vasallo (2006):

$RI_A = 3.0881 \times A^{0.75}$

Where RI_A is the unbiased relative intensity of atresia and A is relative intensity from the present profile counting. Moreover, prevalence of atresia was defined as the number of fish with atresia divided by the total number of examined fish.

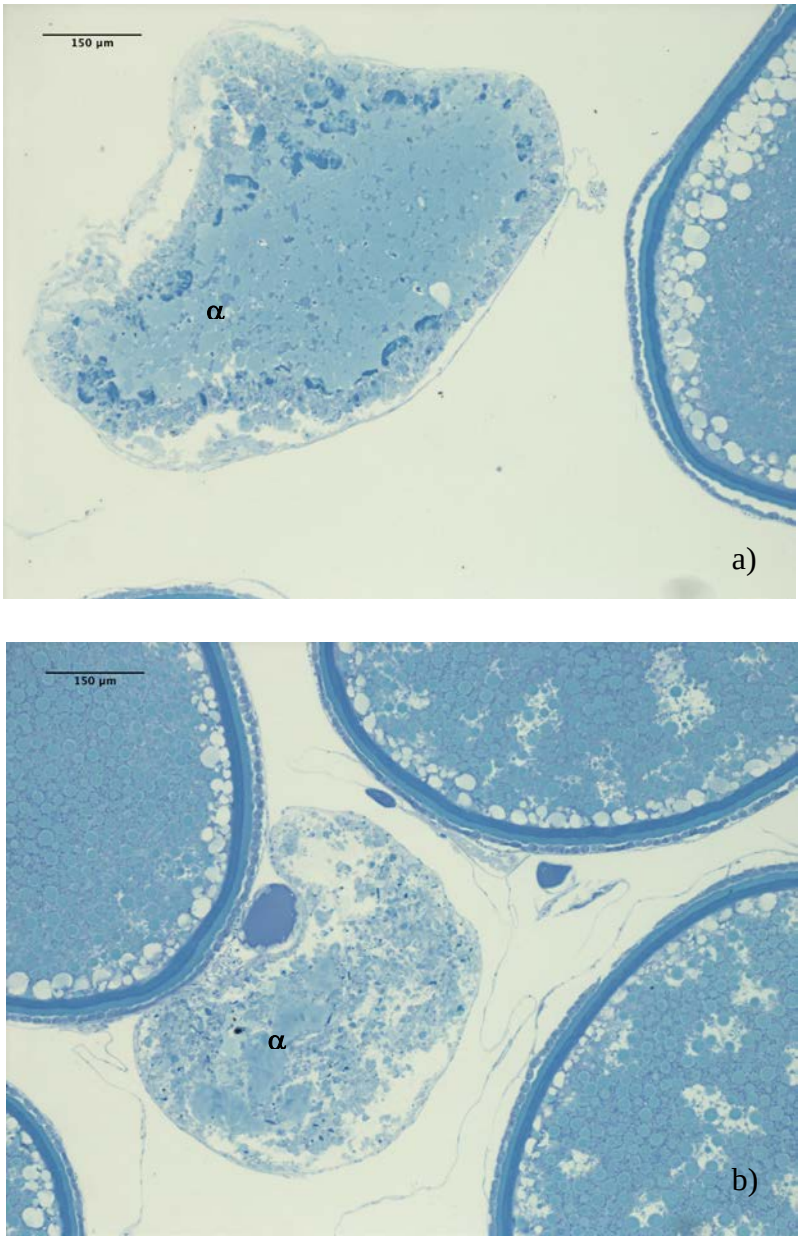

Figure 3. Example of micrographs of α-atretic oocytes for Lindåspollene herring. A developed stage of α-atretic appears in a) and a late stage of α-atretic oocyte is shown in b).

2.6 Calculations and statistics

All statistics were carried out using Statistica 8.0 (StatSoft, Inc., Tulsa, Oklahoma) for Windows XP. All data sets were screened for normality and homogeneity of variance and transformed if they did not follow the parametric assumptions. Student's *t*-test was used to compare mean values of age and *K* between fish groups. Also, differences among fish groups were analysed using one-way ANOVA with a posteriori comparisons (Tukey 95%). ANCOVA (un-transformed data) was carried out to compare weight at length among fish groups for both males and females for each fish group. A regular Welch two-sample *t*-test was used to compare length at age among the groups. Ln-transformed data was used to compare means of GSI among the fish groups. A non parametrical Kruskall Wallis test was used to compare the means of Fulton's *K* among the groups. The parameters from linear and multiple regression analysis are shown in tables. Differences between mean values were considered as significant when $P < 0.05$.

To estimate the fish condition Fulton's condition factor (Nash et al., 2006) was calculated using the following equation:

$$K = 100000 \times TW / TL^3$$

where *TW* is the total fish weight (in grams) and *TL* is the total fish length (in millimeters). The gonadosomatic index (*GSI*) was calculated using the equation:

$$GSI = 100 \times GW / TW$$

where *GW* is the gonad weight (in grams).

Fecundity was defined as the total number of vitellogenic or hydrated oocytes (i.e. still surrounded by the follicle layer) while relative fecundity was defined as the fecundity divided by the total weight of the fish. Fecundity (*F*) was calculated using the equation from Óskarsson et al. (2002):

$$F = 1.708 \times 1010 \times (1.04 \times OW^{0.936}) \times OD^{-2.301}$$

where *OW* is the fresh ovary weight in grams and *OD* the formalin fixed mean oocyte diameter in μm.

Since only fresh ovary weight was registered, a correction factor was added to the original equation to correct for the approximate 4% increase in ovary weight due to fixation (Kennedy et al., 2011).

Because no fecundity information was available for oceanic NSS herring for 2010, fecundity was estimated using the fecundity-length-Fulton's condition (*F-LK*) relationship for NSS herring in the spawning season of 2008 (Kennedy et al., 2011) (see also above):

$F = 617\,L + 80010 \times K - 2.02 \times 10^5$

3 Results

3.1 Length, weight, age, and condition

Except for local Lindåspollene (LP 2009) herring where males showed a higher weight at length (ANCOVA; P=0.0018), there was no difference in weight at length between males and females in each fish group (ANCOVA; $P > 0.05$).

Individuals caught in Lindåspollene were classified as NSS or LP. As explained above, the NSS herring caught outside Lindåspollene (NSSOLP) were analysed separately from the NSS herring caught inside Lindåspollene (NSSILP). NSSILP and NSSOLP showed a very similar age distribution (Figure 4) and the same average age (6 years). On average, both were significantly younger than LP fish (Kruskall Wallis; $P < 0.001$) which had a peak frequency at 15 years old. Neither LP nor NSSILP showed any significant variance in average age from 2009 to 2010.

Overall, LP was the oldest group, followed by local Trondheim (TR) herring (9.7 years average age) and Landvikvannet (LV) as the youngest group (4 years old).

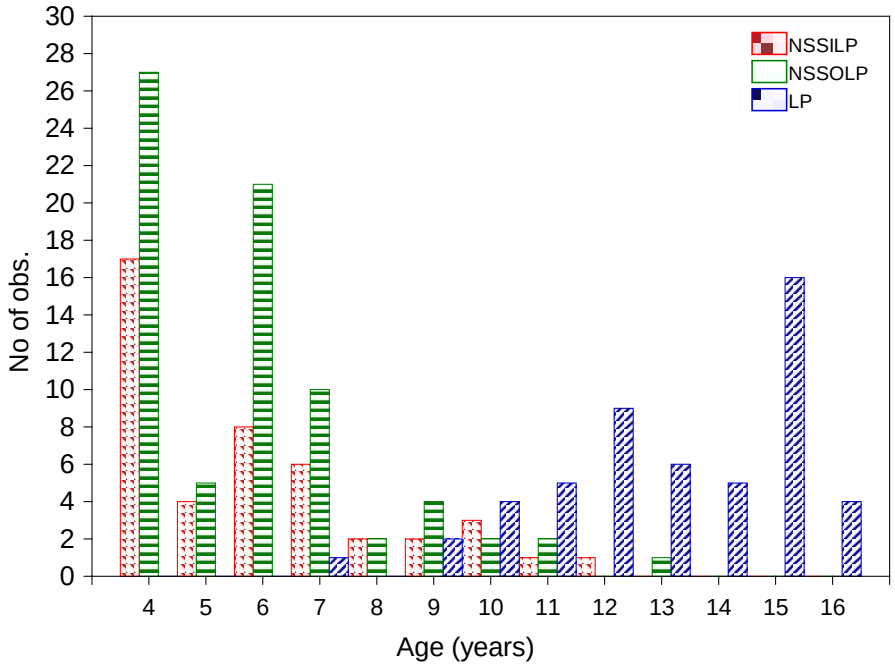

Figure 4. Age distribution by component in Lindåspollene in 2009.

In terms of length-at-age, NSSOLP, LP and NSSILP (samples from 2009) overlapped for ages 7, 9, 10 and 11, although with few data in some groups (Figure 5). Applying a regular Welch two-sample *t*-test, the NSSOLP fish were found to be significantly larger than the LP fish at ages 9 (P = 0.007), 10 (P = 0.011) and 11 (P = 0.006). No differences were found for 7-year-olds (few LP data).

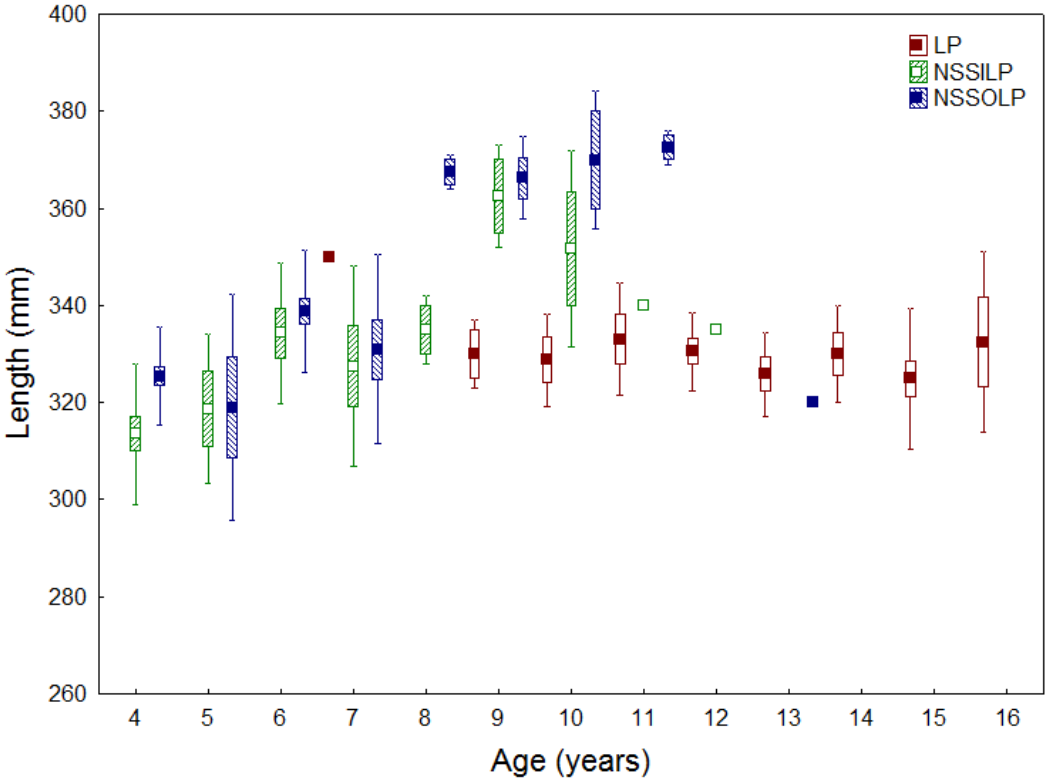

Figure 5. Mean total length (mm) at age for each group in Lindåspollene 2009. Boxes and whiskers represent standard error and standard deviation, respectively.

In 2010 when comparing the Lindåspollene samples only, individual length-at-age comparison was not appropriate for most of the age groups due to incomplete datasets. It was only possible to compare LP and NSSILP at age 9 (with n = 3 for both LP and NSSILP). However no significant difference was found (Welch *t*-test; P = 0.768). The largest herring recorded in Lindåspollene was a 38 cm NSSOLP herring caught in 2009.

Comparing the length-at-age among the other populations sampled in 2010 (Figure 6), oceanic NSS herring was typically the largest group, followed by the local LP, LV and TR herring. Due to incomplete datasets length-at-age was only compared among NSS,

LP and TR at age 11. The test indicated that a NSS herring was significantly bigger than a LP herring (Welch *t*-test; $P = 0.001$) and that a TR herring was significantly smaller than a LP herring (Welch *t*-test; $P < 0.001$).

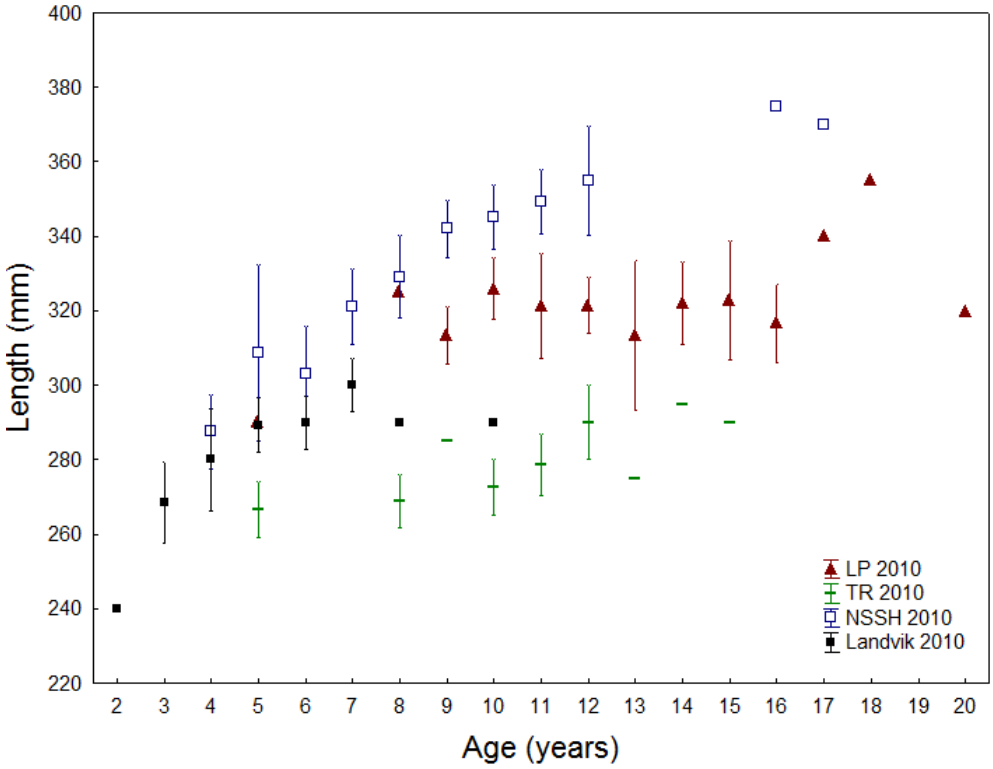

Figure 6. Mean length (mm) at age by population in 2010. Whiskers represent 95% confident interval.

Fulton's condition factor (*K*) was independent of length in all groups (linear regression; $P > 0.05$; $r^2 < 0.04$) and ranged from 0.64 to 1.05. Regarding the samples caught in 2009 in Lindåspollene, NSSOLP had a significantly lower mean value of *K* than LP and NSSILP (Kruskall Wallis; $P < 0.001$), but there were no differences between the later ones (*t*-test; $P = 0.448$) (Figure 7).

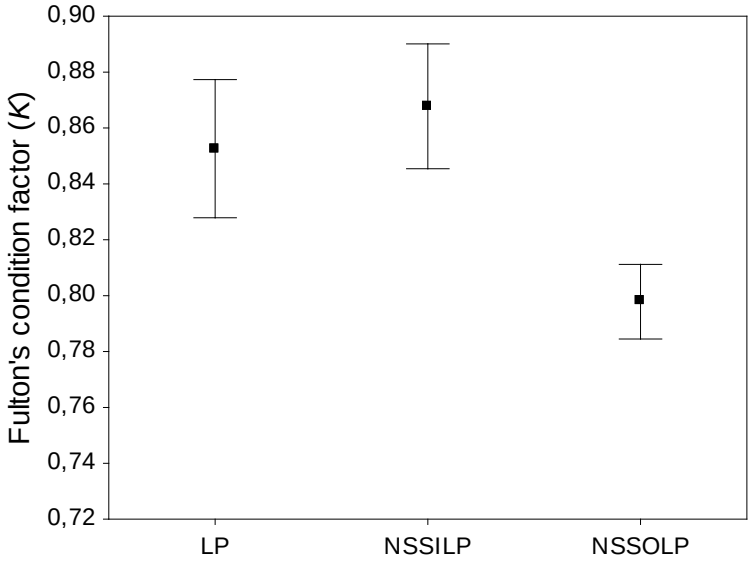

Figure 7. Mean K for Lindåspollene samples caught in 2009. Whiskers represent 95% confidence interval.

In relation to the condition of the samples caught in 2010 (Figure 8) NSS herring presented the highest mean value of *K*, although not significantly higher than LV (*t*-test; $P = 0.552$). No significant difference was found between the mean condition value of LP and NSSILP (*t*-test; $P = 0.3611$). TR herring presented a mean condition value ($K = 0.75$) significantly lower compared to all other groups (ANOVA; $P < 0.001$) and 17% of the individuals had *K* bellow 0.7. Herring presenting $K < 0.7$ are considered as being in low condition and high levels of atresia are common in fish this level (Óskarsson et al., 2002). From 2009 to 2010 the condition of both LP and NSSILP decreased significantly (*t*-test; $P < 0.001$ and $P = 0.004$ respectively).

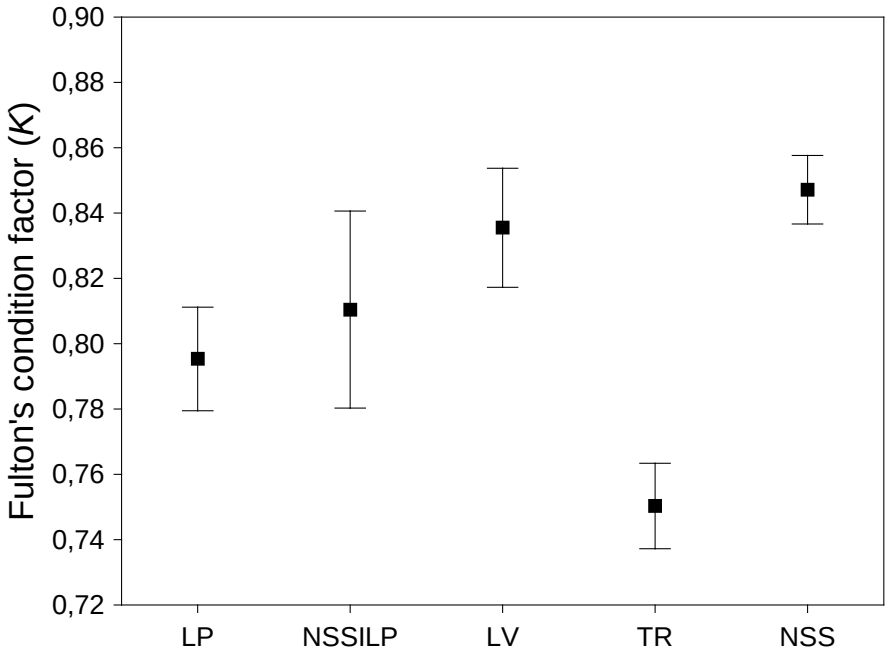

Figure 8. Mean *K* for samples caught in 2010. Whiskers represent 95% confidence interval.

Table 2.
Length, age, condition and LC oocyte diameter of the sampled female fish.

Stock	Year	*n*	Length (mm)				*n*	Age (years)				n	*K*				*n*	LC oocyte diameter (µm)			
			Mean	SD	Min	Max		Mean	SD	Min	Max		Mean	SD	Min	Max		Mean	SD	Min	Max
LP	2009	53	330	10,5	310	355	51	13	2,2	7	16	53	0,85	0,09	0,67	1,05	53	1163	98	973	1319
	2010	69	322	12,5	285	355	68	12,5	2,5	5	20	69	0,80	0,07	0,64	0,96	69	1061	61	915	1160
NSSILP	2009	45	326	19,8	285	370	44	6	2,2	4	12	45	0,87	0,07	0,67	1,00	45	1171	112	914	1393
	2010	21	318	15,8	285	340	21	7,1	1,9	4	10	21	0,81	0,07	0,71	0,96	21	1093	70	954	1286
NSSOLP	2009	84	335	19,4	295	380	74	5,9	2,0	4	13	84	0,80	0,06	0,67	0,94	84	1189	98	787	1399
TR	2010	60	274	9,7	250	300	60	9,6	1,9	5	15	60	0,75	0,05	0,66	0,91	59	1133	50	1043	1307
LV	2010	58	277	15,5	240	310	58	4,2	1,6	2	10	58	0,83	0,07	0,70	1,00	58	1173	60	1032	1333
NSSH	2010	134	322	21	275	375	129	7,5	2,1	4	17	134	0,85	0,06	0,66	0,99	-	-	-	-	-

3.2 Historical growth data

The analysis of the historical data on length-at-age showed no information on young (2 to 4 years old) LP. Still, with the available data, it seemed that LV and LP had similar growth rates while NSS presented a considerable higher growth rate. At the age of 2 the NSSILP had the highest average length (26 cm) but at age 7 NSS is the largest. TR herring showed the lowest growth rate. At age 5 a TR fish was 26 cm while an oceanic NSS was on average 31 cm. At the same age, a LP and a LV herring were 30 and 29 cm, respectively. Oceanic NSS herring reaches a larger maximum size compared to the other herring populations.

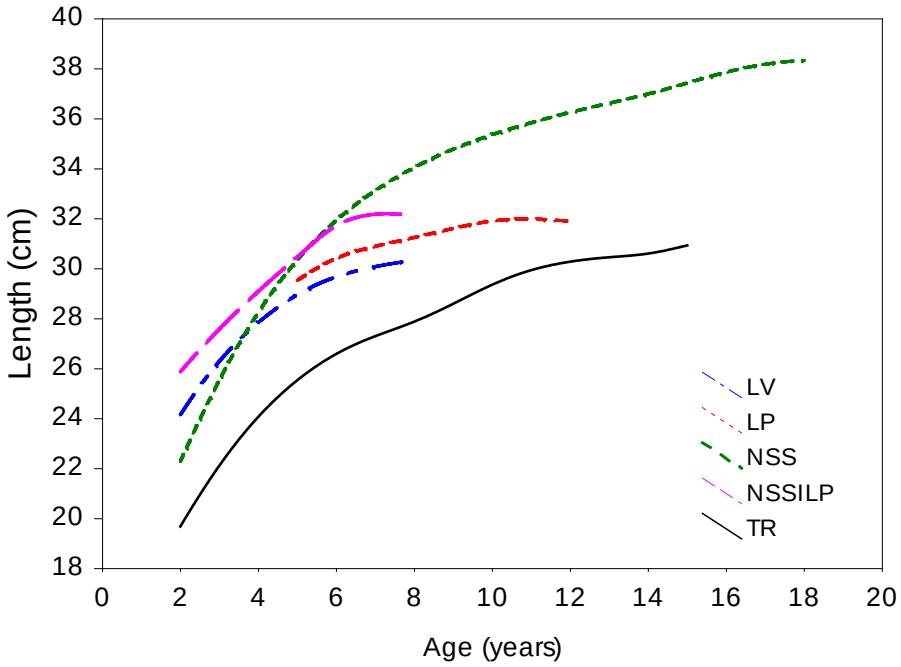

Figure 9. Growth in length for herring from Landvik (LV), Trondheim (TR) and oceanic NSS collected from the IMR database. Data on local Lindåspollene (LP) and NSS herring caught inside Lindåspollene (NSSILP) from Johannessen et al. 2009.

3.3 GSI and LC oocyte diameter

There was a significant difference in GSI (ANOVA; $P < 0.01$) between the locations. The GSI of TR herring was significantly higher than in all other groups (ANOVA; $P < 0.05$) except when compared to the samples of LP herring caught in 2009 (Tukey test; P

= 0.32). NSSOLP had clearly the lowest GSI (ANOVA; $P < 0.001$) followed by the oceanic NSS herring and LP herring. The GSI of LP herring decrease significantly from 2009 to 2010 (Tukey test; $P < 0.001$).

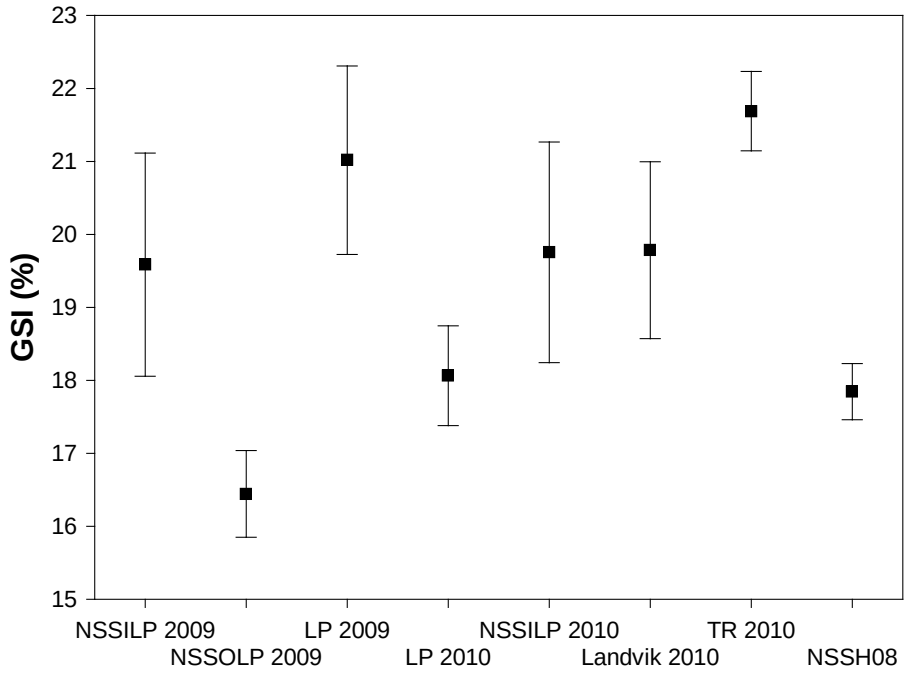

Figure 10. Mean gonadosomatic index (GSI) by location. Whiskers represent 95% confidence interval.

All samples were caught close to the start of spawning so most of the fish had advanced developed oocytes (LC ranged from 700 μm to 1400 μm). Still, there were significant differences in the LC oocyte diameter between the samples (ANCOVA; $P < 0.001$) indicating a difference in maturity stage among the groups (Figure 11). The LC oocyte diameter of LP and NSSILP from 2009 was significantly lower compared to all other groups (ANOVA; $P < 0.001$) but without any significant difference between the two (Tukey test; $P = 0.71$).

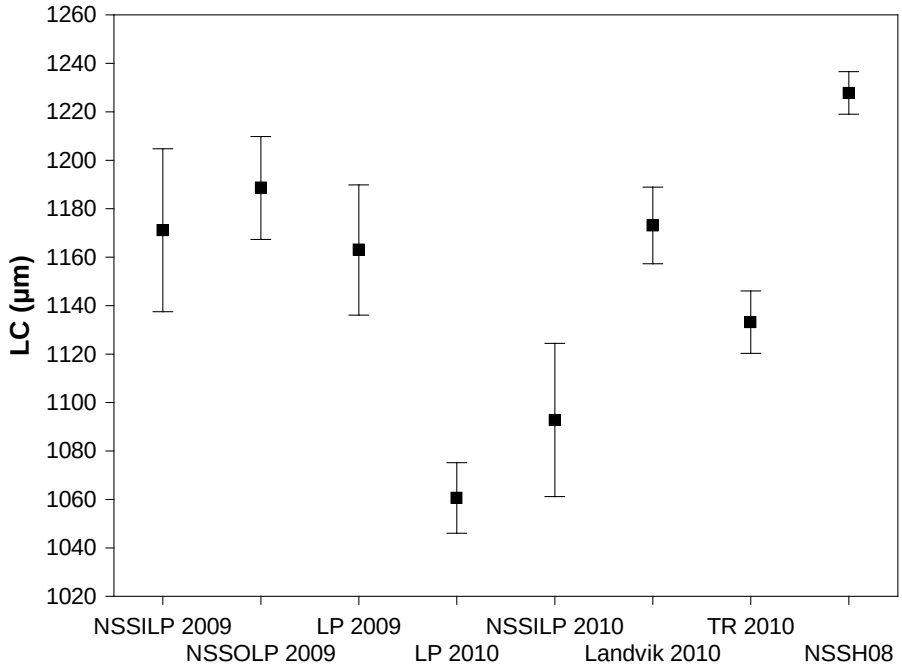

Figure 11. Mean leading cohort (LC) oocyte diameter by location. Whiskers represent 95% confidence interval.

3.4 Potential fecundity

Potential fecundity increased with whole body weight for all fish groups (Figure 12). LP and NSSILP presented significantly higher potential fecundity compared to all other groups (ANOVA; $P < 0.001$) but did not differ from each other (Tukey test; $P > 0.05$). Potential fecundity of NSS herring in 2010 was significantly lower than in 2008 (Tukey test; $P = 0.008$) (Figure 13). NSSOLP (2009) and NSS herring (2008) showed a similar value of potential fecundity (Tukey test; $P > 0.05$). LV and TR had the lowest values of potential fecundity but did not differ from each other (Tukey test; $P > 0.05$). As fecundity differences can be result of the development stage of the ovary the LC oocyte diameter was included as a covariate in the regression models. This resulted in a slightly decrease in the overall potential fecundity but the main pattern was maintained.

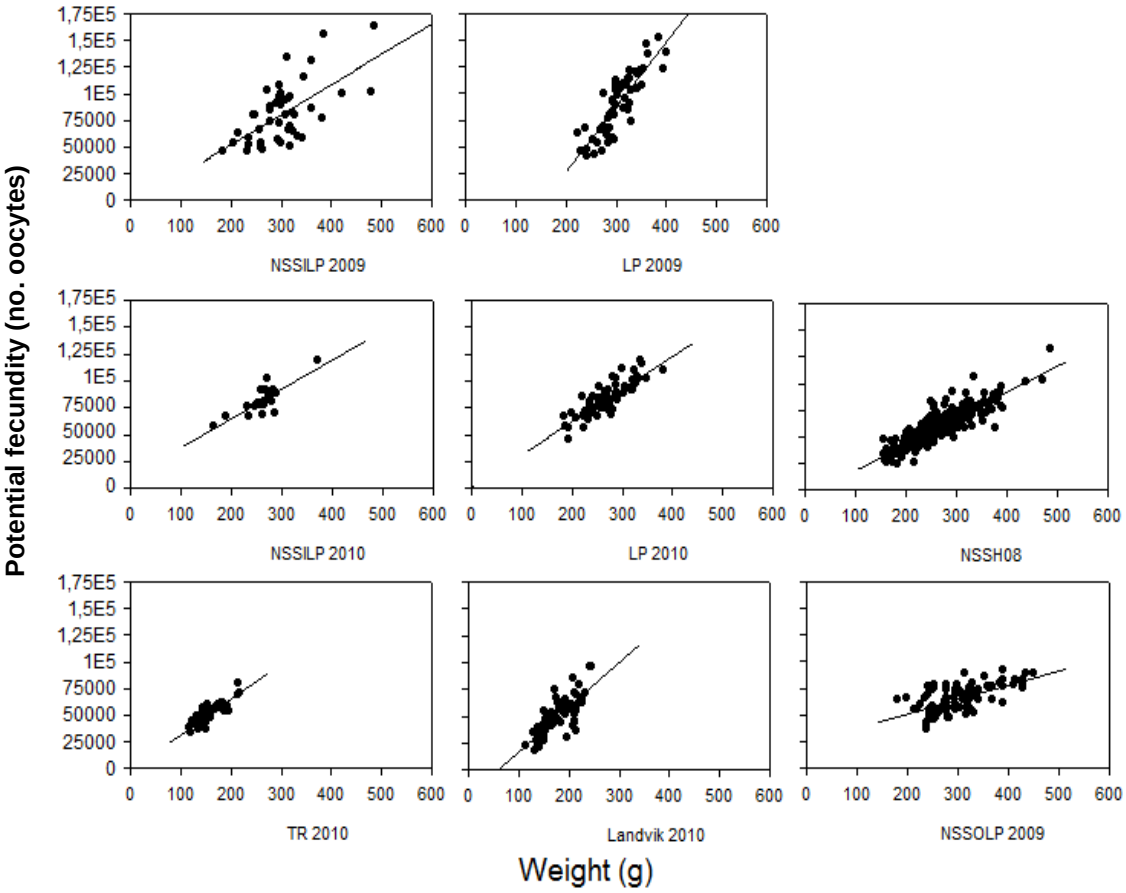

Figure 12. Relationships between potential fecundity and whole body weight for each fish group. Each point represent one individual.

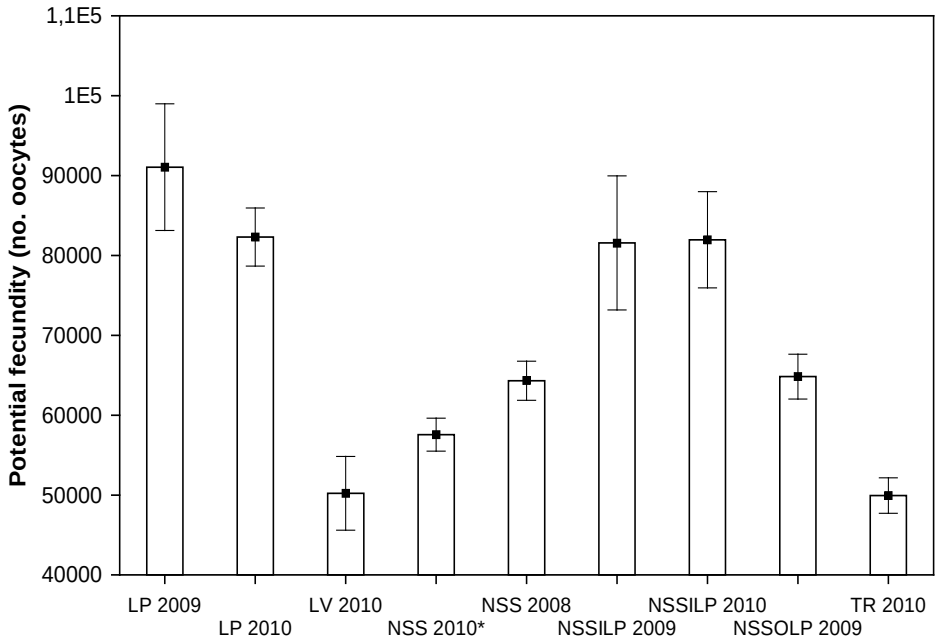

Figure 13. Mean potential fecundity for each fish group. Whiskers represent 95% confidence interval. Estimated potential fecundity is marked with *.

Potential fecundity regressions were made for all populations and all years (Table 3). Weight always explained potential fecundity better than length. Weight was used as an independent variable, either alone or in combination with LC oocyte diameter (W-LC). When LC oocyte diameter was included as an additional independent variable the explanatory power (r^2) increased in all cases. The addition of age (A) to the model (W-A-LC) did not add any significant changes to any of the groups, except for NSS herring (Multiple regression; $P < 0.001$). Potential fecundity seemed to increase significantly with increasing age, specially for migratory NSS herring, NSSILP (2009), NSSOLP, TR and LV herring (linear regression; $P < 0.001$). However, relative fecundity was not related to age in any of the populations (see below).

Table 3.
Potential fecundity regressions split by stock and year using weight (W), length (L), age (A) and LC oocyte diameter (LC) as independent variables. Non significant values are signalized as "ns".

Location	year	n	W-r^2	L-r^2	A-r^2	W-LC-r^2	W-A-LC-r^2
LP	2009	51	0.736	0.143	ns	0.804	0.803
	2010	69	0.714	0.575	ns	0.732	0.708
NSSILP	2009	45	0.399	0.238	0.221	0.487	0.499
	2010	21	0.652	0.633	ns	0.658	0.670
NSSOLP	2009	84	0.401	0.289	0.277	0.599	0.587
TR	2010	59	0.731	0.549	0.255	0.832	0.835
Landvik	2010	58	0.569	0.266	0.259	0.769	0.772
NSS	2008	253	0.773	0.708	0.470	0.822	0.829

3.5 Relative fecundity

The relative fecundity for all stocks, except for NSSILP (2010), decreased significantly as the LC oocyte diameter increased towards the start of spawning (Figure 14). The non-significance variance in relative fecundity with increase of the LC oocyte diameter for NSSILP (2010) could be explained by the few data present in this group ($r^2 = 0.069$; n=21). Because the relative fecundity most often decreased significantly as time of

spawning became closer (indicated by increasing LC oocyte diameter), the LC oocyte diameter was included as one of the independent variables in the fecundity regressions model. A LC oocyte diameter value of 1100 µm was used as a normalizing setting when the output from the model was calculated. There was no significant effect of age on relative fecundity for any of the populations (linear regression; $P > 0.05$, $r^2 < 0.12$).

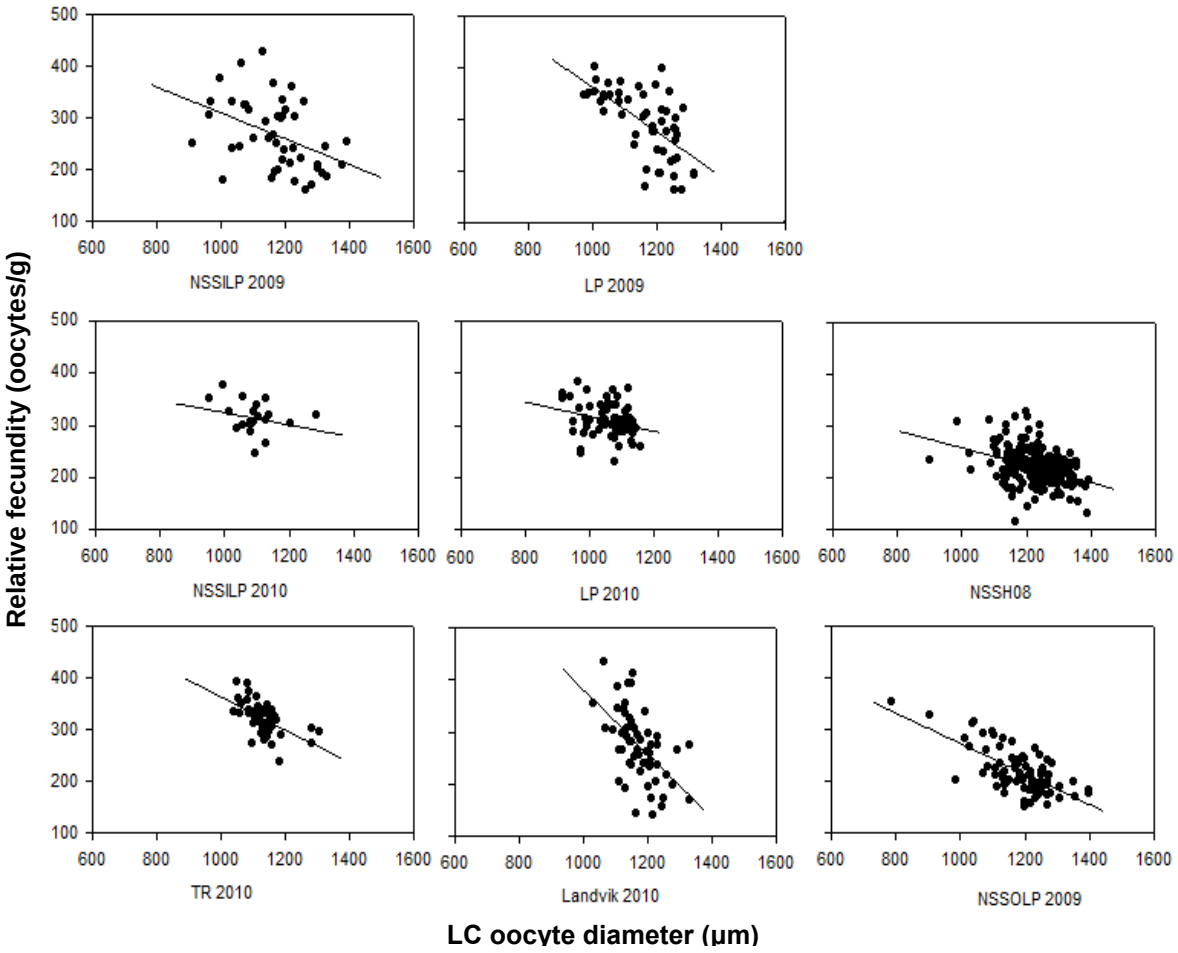

Figure 14. Relative fecundity (number of oocytes divided by total fish weight) versus LC oocyte diameter for each sampling location. Each point represent one individual.

When the relative fecundity was compared between the groups (Figure 15), it was found that the NSSOLP females and the oceanic NSS (both 2008 and 2010) were significantly less fecund than all other groups (ANOVA; $P < 0.001$) but not significantly different from each other ($P = 0.99$). Both within the year of 2009 and 2010 the NSSILP showed no significant difference in mean relative fecundity when compared with the locals (LP) (Tukey HSD test; $P = 0.08$, $P = 0.99$). However the relative fecundity of each group varied from one year to the next, specially for NSSILP, which showed a significant

higher relative fecundity in 2010 (P = 0.001). The local TR presented the highest mean (321 oocytes/g) relative fecundity of all the groups. When the LC diameter was used as a fixed covariate value (1100 μm) the general pattern in relative fecundity was maintained. A relative fecundity threshold value of approximately 270 oocytes/g seemed to separate NSSOLP and the oceanic NSSH from the other groups following standardization by maturity (LC oocyte diameter).

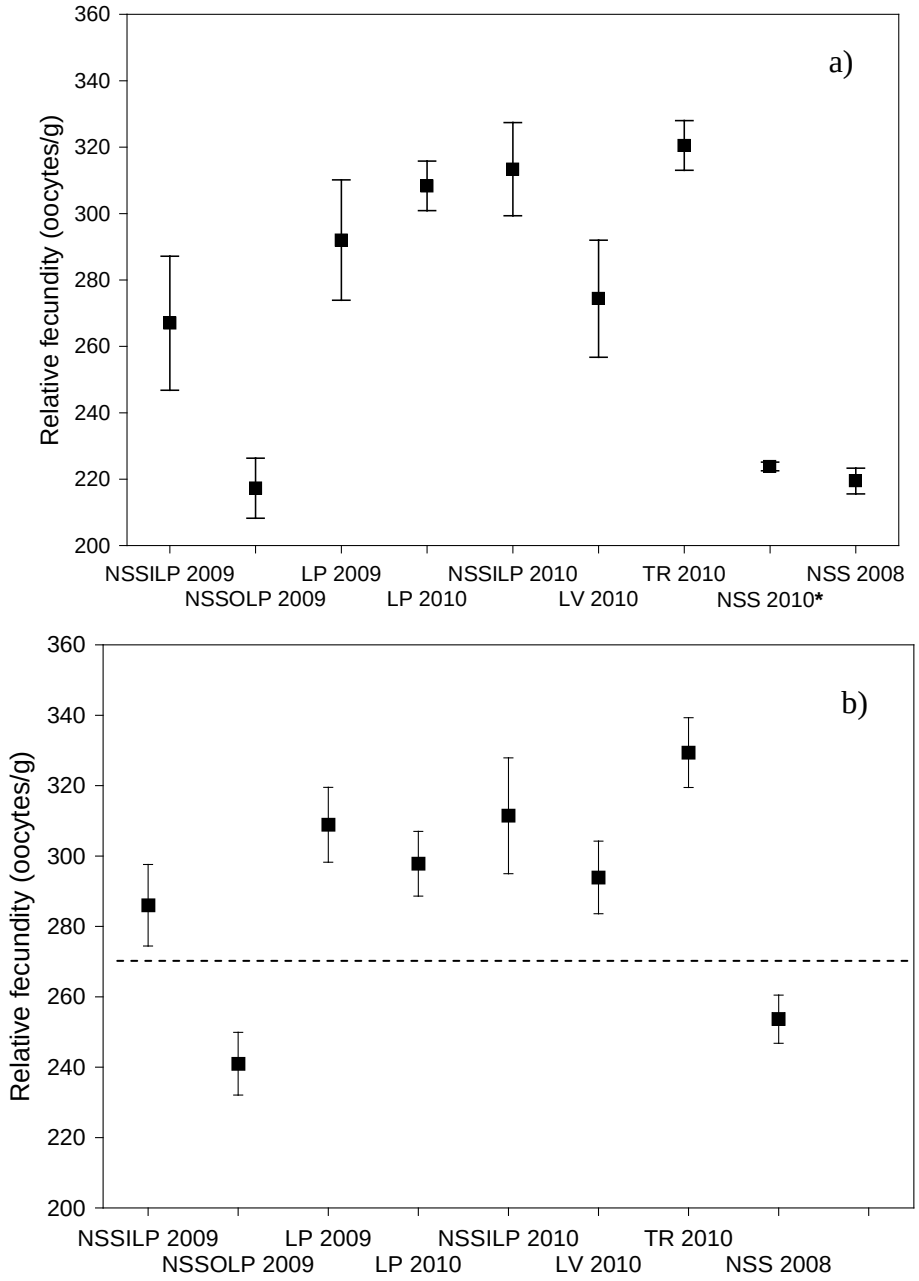

Figure 15. Mean relative fecundity by stock a) and mean predicted relative fecundity (model output) calculated for a LC oocyte diameter of 1100 μm b). For NSS 2010 there was no oocyte measurements available so data from 2008 is shown. Estimated relative fecundity is marked with *. Dashed line suggests a threshold separation value. Whiskers represent 95% confidence interval.

The relative fecundity for a 250, 300 and 350 mm fish was also calculated from the model that included both length and LC oocyte diameter as independent variables, again the mean oocyte diameter was set to 1100 μm. Because of length differences between the groups, the relative fecundity was not calculated for values outside each group's length range. When comparing oceanic NSS herring with the NSSOLP, a 300-mm herring from the two populations was almost equally fecund and both were still considerably less fecund than all other groups (Table 4).

Table 4.
Model output on relative fecundity (oocytes per gram of body weight) by location and length. Values were calculated from regression models using length and LC oocyte diameter as independent variables. To calculate the output, a fixed LC oocyte diameter of 1100 μm was used.

Length (mm)	LP	LP	NSSILP	NSSILP	NSSOLP	NSS	Landvik	Trondheim
	2009	2010	2009	2010	2009	2008	2010	2010
250							286	318
300		295	286	312	252	234	367	347
350	323	312	284		236	255		

3.6 Atresia

In 2009, NSSOLP and NSSILP showed a percentage of fish with atresia (i.e. prevalence) of atresia of 11 and 14%, respectively. In the same year no atresia was found in LP. In 2010, prevalence of atresia was 20 and 60% for TR and LP females, respectively (no NSS herring were analysed in 2010).

The average intensity of atresia (RIA) was 8 and 4% in NSSOLP and NSSILP (both from 2009), respectively. In 2010, TR and LP had an average RIA of 4 and 6%, respectively. Overall, the maximum level of RIA (12%) was found in one LP individual caught in 2010 which also had a low condition factor (K = 0.64).

4 Discussion

This study compared herring populations with rather different life history strategies. The results from length-at-age showed that local and stationary populations grow slower than the migratory population of oceanic herring. The relative fecundity was also markedly different between these two types of populations. Overall, these results strongly suggest that the energetic cost of body growth and/or spawning migration in Norwegian spring spawning (NSS) herring have a direct negative effect on relative fecundity. However, changes in fecundity may not always be associated with reproductive investment since both the number and size of the eggs spawned by a female contribute to her reproductive success (Bagenal, 1973).

The present results suggest that for migratory NSS herring the cost of growing faster is reduced fecundity. Although many possible trade-offs between life history traits have been identified (Stearns, 1992), the trade-off between body growth and reproduction is among the most important in fishes (Roff, 1983) as fecundity is generally an increasing function of body size (Wootton, 1984). Moreover, in NSS herring the energy loss during migration is known to decrease with size (Slotte, 1999a). This is due to fact that metabolic rate decreases with body sized (Winberg, 1961) and the optimal swimming speed (velocity at which the total energy expenditure per unit distance travelled is minimal) increases with the fish size (Ware, 1978). Consequently, it seems advantageous for migratory NSS herring to allocate more energy into growth with present fecundity as the result of the trade-off. On the other hand, the potential for future reproduction may increase because, as fish grow larger, the cost of migration decrease and fecundity increases. These results are in agreement with the findings of Tsikliras et al. (2007) where a negative relationship between growth rate and fecundity was also found for round sardinella (*Sardinella aurita*).

However, in this study migratory NSS herring was compared with non-migratory herring populations and the energy cost of migration may also affect fecundity. The results from relative fecundity indicate that migratory NSS individuals produce significantly less oocytes per gram of fish compared to the non-migratory ones. This is likely to be because the energy allocated to migration reduces the energy available for egg production (Glebe and Leggett, 1981). A trade-off between migration costs and

reproduction was also found in the South American characin *Procilodus mariae*, where stationary females allocate five time as much energy to egg production as do females that undertake up-river migration (Saldana and Venables, 1983). The great energetic cost of spawning migrations is also well documented for the anadromous American shad *Alosa sapidissima* (Leggett and Carscadden, 1978). In this case a reduction of the energy allocated to gonad production, with a corresponding reduction in relative fecundity, resulted in a bigger allocation of energy to somatic reserves needed to complete the migration towards the spawning grounds and return to the feeding areas.

Life history studies are based on the hypothesis that animals have limited amount of energy and that optimum life history strategy allocates resources to growth, maintenance and reproduction in a way that maximizes new and viable offspring (Roff, 1983; Stearns, 1992). With this assumption, it is likely that the differences found in the relative fecundity of migratory and non-migratory herring populations are related to geographical differences in juvenile survival. Slotte and Fiksen (2000) have shown that the reproductive strategy of migratory NSS herring is based on the fact that the great energetic cost of the spawning migration has less importance compared with the possibilities of better larvae survival in southern areas of the Norwegian coast.

For all fish groups except the NSS herring caught inside Lindåspollene (NSSILP) in 2010, relative fecundity decreased as time of spawning became closer, indicated by increasing leading cohort (LC) oocyte diameter. Down-regulation of fecundity by absorption of oocytes through atresia is a known mechanism in Atlantic herring (Kurita et al., 2003; Óskarsson et al., 2002) and also common in other determinate spawners like cod *Gadus morhua* (Thorsen et al., 2006). Kurita et al. (2003) found that the largest decrease in fecundity occurred between July and October but also that fecundity continued to decrease between October and Jannuary. This contrasts with results found by Kennedy et al. (2011) who found that fecundity did not decrease between overwintering and spawning. Overall, down-regulation may occur throughout the whole maturation period (van Damme et al., 2009) and shorter intervals of sampling seem to be very important to acquire a precise picture of fecundity regulation (Kurita et al., 2003). This was beyond the scope of this study. Only a pre-screening process was performed where a few samples were analysed to examine the levels of atresia. Nevertheless, all samples were caught very close to spawning and relative fecundity

was compared among groups with standardized LC oocyte diameter, i.e. similar point in ovary development.

Some studies indicate that there is a general positive association between potential fecundity and condition of NSS individuals (Slotte, 1999b; Slotte et al., 2000). However, when comparing the mean condition of each studied population it was found that Trondheim herring presented the lowest value of *K*, even significantly lower than the NSS herring. Since Trondheim herring was one of the most fecund populations, it seems contradictory that this population has very low condition. However, Fulton's *K* is based on the assumption of isometric growth which is not valid for all fish (Stevenson and Woods, 2006). Since this population has a major difference in size (mean average of 27 cm) comparing with oceanic NSS herring (mean average of 32 cm), a direct comparison of *K* between them may not be fully appropriate (Cone, 1989). In addition, other studies have shown that Fulton's condition factor *K* cannot give precise or consistent measures of muscle fat content in herring (Davidson and Marshall, 2010; McPherson et al., 2011).

Nevertheless, in a historical perspective and comparing to previous studies (Óskarsson et al., 2002) the body condition of the studied oceanic NSS herring was rather good (>0.70) considering having undertaken a costly migration distance to the spawning grounds. This outcome could be explained by Slotte and Fiksen 2000 who have compared the energetic cost of different spawning migratory distances in NSS herring. and found that those swimming longer distances to the south had higher fecundity than those spawning at closer locations to the wintering area. However, this was related to the fact that only the largest and in better condition individuals could afford to reach the southern spawning areas (Slotte and Fiksen, 2000).

The fact that NSS herring that have migrated longer distances to spawn have higher fecundity compared to the ones that migrated shorter distances (Slotte and Fiksen, 2000) is only indicating a more optimal use of energy by larger individuals and does not have to be contradictive to the present results. First, since NSS herring have a higher body growth rate compared to the local populations, allocation of energy is presumably redirected from reproduction to growth. And second, stationary and well isolated herring populations are most likely to have developed a different and specific life history strategy (Stearns, 1992). I.e., comparing to a stationary population, any NSS

herring has to allocate more energy into body growth and spawning activities with a reduction in egg production as consequence.

For the present study, and like in Johannessen et. al. (2009), NSS herring caught outside Lindåspollene (NSSOLP) was analysed separately from the NSS herring caught inside Lindåspollene (NSSILP) since a higher contribution of "strange herring" is likely to occur in this area (see Introduction).

Except for the bimodal age distribution, very small differences were found between the NSSILP herring and the locals (LP) in all of the studied characteristics. On the other hand NSSOLP were in considerably poorest condition and less fecund. Both in 2009 and 2010, the NSSILP herring was not significantly larger at age than LP herring. This contrast with the results found by Johannessen et. al., (2009) who found that NSS herring caught within the school inside Lindåspollene to be significantly larger when compared to the local herring. This difference could be explained by 1) Johannessen el. al (2009) compared LP and NSSILP based only on samples caught from the same school while in the present study all samples caught inside Lindåspollene (inside or outside the school) were pooled together. By doing this, more types of herring could have entered in our NSSILP group (resulting in a higher variance of sizes in some age-groups), 2) the high variance in size in the NSSILP herring would likely lead to a non-statistical difference between this group and LP, 3) both studies had few data available for the length at age comparisons and any statistical result would not be very robust. 4) Also, it is also important to note that gill nets with the same mesh size were the main fishing gear to catch all samples. Thus, fish size is not expected to be very different.

Gear size selectivity could also explain the high frequency of young NSSILP and NSSOLP and the absence of (young) LP individuals, which is in line with the smaller size at age of LP group.

Atlantic herring is known to have a highly complex population structure and different stocks can exhibit variation in several life-history parameters (Clausen et al., 2007). This study is the first to assess the fecundity of the herring components spawning in Lindåspollene. Overall, the combination of the present results on relative fecundity and the difference in vertebrae counts (Lie et al., 1978) suggest that the particular herring component classified as NSSILP, is not composed of true oceanic NSS herring. Lindåspollene is suggested to be one of many coastal spawning grounds for NSS

herring. Thus, it is not unlikely that more than one herring sub-population mix in this area at this time of the year or even for longer periods (Johannessen et al., 2009).

The bimodal age-frequency distribution suggesting two groups was also found in Johannessen et al. (2009) who suggested that the migratory component might just return to Lindåspollene to spawn until it has outgrown the local/resident group. However, looking at the present fecundity results, it seems more likely to assume the existence of a migratory component that will gradually cease to migrate out of Lindåspollene and in the long term mix completely with the resident component. This was also hypothesized by Johannessen et al. (2009). Their study was, however, without knowledge of fish condition and fecundity.

Let us imagine that, NSSOLP are some "strange" herring (most likely oceanic NSS herring) coming from wintering areas far away to spawn near Lindåspollene. They would have spent energy on the migration and possibly arrive in a lower state of condition, thus be less fecund. Moreover, part of this group of herring (possibly most younger individuals) could penetrate farther in the area of Lindåspollene (NSSILP) and spawn together with the locals. Then, some of these individuals may stop migrating outside of Lindåspollene after spawning and adapt to the same environment as the locals. These herring would still be larger at age compared to the locals and show similar type of otolith pattern as do NSS. After years without long migrations they may save energy and be more fecund than the new migratory ones. This is, if migratory herring stays in Lindåspollene for the next spawning season, they would still be identified as NSS herring (otolith pattern) for some years but quickly experience condition and fecundity as the locals. This could explain why this group shows a high and comparable condition and fecundity with the local ones; similar life style is linked to similar environmental conditions

Regarding the NSSOLP herring, since they were larger at age compared to the locals and the relative fecundity was similar to migratory NSS herring (both with relative fecundity bellow 270 oocytes/g) it is more likely that NSSOLP is in fact oceanic NSS herring which migrate to Lindåspollene to spawn.

In summary, this study underlines the importance of the species-specific life history adaptations in the reproductive output in populations of Atlantic herring. For NSS herring size is an important feature for optimal use of energy for migration and

migration to southern areas increases larvae survival. On the other hand, non-migratory herring populations are adapted to a stationary life style where the energy cost of a higher growth rate may not be compensated. This supports the findings of Atlantic herring exhibiting a large dynamic range of reproductive strategies which are in turn a reflection of population adaptations to their environment. Moreover, it is also suggested that migratory species may produce fewer number of eggs compared with stationary ones. However, futures studies should also include egg size information to evaluate the female total reproductive investment.

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