Strategies for partition between body growth and reproductive investment in migratory and stationary populations of spring-spawning Atlantic herring (Clupea harengus L.)

Filipa F.G. Silva a,b,*, Aril Slotte b, Arne Johannessen a, James Kennedy c, Olav Sigurd Kjesbu b

a University of Bergen, P.O. Box 7803, Thormaehlengt. 53 A/B, 5020 Bergen, Norway
b Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway
c Mareforsking Marin, P.O. Box 3675, 8021 Ålesund, Norway

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ABSTRACT

In this study the reproductive investment of six populations of Atlantic herring (Clupea harengus) in Norwegian waters was contrasted in relation to trade-offs with body growth (relatively slow–relatively fast) and migration distance (stationary-migratory). Down-regulation of fecundity through the process of atresia as well as standardisation of fecundity to the prespawning stage were included as process-oriented reproductive factors, applying both histological and image analysis techniques. The further analysis included historic information on body growth as well as published information on fecundity from several stocks in the North Atlantic. The Norwegian spring-spawning (NSS) herring could be split into three sub-components: migratory (oceanic), likely semi-stationary (coastal) and stationary. The latter one as well as three other populations were sampled in relatively isolated semi-enclosed areas (pond, “lake” or fjord). The study documented clear signs of trade-offs: migratory herring had a significantly higher growth rate and lower relative fecundity while stationary populations grew slower and presented higher values of relative fecundity. So these traits appeared highly plastic and for the first time explicitly demonstrated in the three types of NSS herring: stationary NSS herring had high fecundity and body condition while the truly migratory counterpart was low in both while the intermediate version was low in fecundity but high in condition. The literature-based analysis of other Atlantic spring-spawning herring populations seemed to corroborate the finding that slow-growing herring is relatively more fecund than the faster-growing populations.

1. Introduction

Considerable attention has been directed towards the quantitative patterns present in fundamental life history parameters of marine fishes (Kawasaki, 1980; Roff, 1984; Winemiller and Rose, 1992; McCann and Shuter, 1997; Rochet, 2000). 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). Within the same species, sub-populations often occupy a wide range of different habitats and some of the considered traits may vary, reflecting manifestation of different life history tactics. Intraspecific variation in life history characteristics, i.e. plasticity, has 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).

The principal objective of a reproductive strategy is to maximise life time production of offspring which again should successfully produce new progeny (Kjesbu and Witthames, 2007). In fish without parental care this is normally achieved by increasing both offspring number and their quality, both being inherent elements of the concept of Stock Reproductive Potential, SRP (Trippel, 1999). However, the environment, and particularly food availability, is usually unstable. To accommodate the shortage in energy allocated to reproduction, fish may regulate fecundity through atresia or shortening the spawning migration, both features being observed in herring (Slotte, 1999a; Kurita et al., 2003). Since life history strategies are the primary reactions to environmental change, they can be used to classify standard population responses (King and
McFarlane, 2003). It is therefore of importance to obtain such information as part of studies on population resilience, and the formation of new year-classes.

As for many other species, a general distinction can also be made for Atlantic herring between stationary and migratory stocks. However, herring population dynamics are extremely complex including different reproductive strategies, spawning seasons (spring/autumn) and spawning area characteristics (Husebø et al., 2005; van Damme et al., 2009; Gefen, 2009). In Norwegian waters, the stationary populations are, seemingly, self-contained units inhabiting small and semi-enclosed fjords along the coast, but have rarely been studied (Holst et al., 2004). Stationary herring usually have specific growth characteristics differing from their oceanic counterparts that undertake long migrations (Lie et al., 1978). In this study we considered four populations of Atlantic herring, i.e. three stationary herring populations, Lindåspollene, Trondheimsfjorden and Landvikvannet, along with the adjacent, well-studied, migratory Norwegian spring-spawning population. Only the latter population supports a commercial fishery (Tjelmeland and Røttingen, 2009). The others are protected by regulatory measures due to their very small population sizes and are therefore only targeted in recreational fisheries.

Lindåspollene is a semi-enclosed marine system connected with the outer sea via a narrow sill. The small stationary population of herring from Lindåspollene (LP) has a slower growth rate, lower mean number of vertebrae and smaller size-at-age than Norwegian spring-spawning (NSS) herring (Lie et al., 1978). Recent studies (Johannessen et al., 2009) have also shown that more than one herring component is present in this area during the pre- and spawning season. The occurrence of a stationary herring population in the inner parts of Trondheimsfjorden (TR) was first addressed by Broch (1908) and later by Runnstrøm (1941), who demonstrated that this herring was comparatively smaller and with lower vertebral number than NSS herring. More recent studies using allozymes and DNA markers have given support to that TR herring is genetically distinct from NSS herring and other Atlantic populations (Jørstad and Naevdal, 1983; Turan et al., 1998). The herring from Landvikvannet (LV) seems to be a separate population from nearby spring spawners in the Skagerak area due to the low mean vertebral count (second author, unpublished data). There is no evidence that herring actually spawn in this special location, originally a fresh water lake, but connected to the sea by a 3-km long canal in 1880. Our study is the first to report data on growth and reproduction of TR and LV herring, as well as for LP herring in terms of reproduction.

The NSS herring is a highly migratory population, and is one of the largest and most important single fish stock units in the North Atlantic ecosystem (Dragesund et al., 1997). In recent years, the distribution of adult NSS herring has covered a large part of the Norwegian Sea during the feeding period (April–August), while spending the wintering period (September–January) in the Lofoten/Vesteralen area, northern Norway (Huse et al., 2010). In mid-January the stock starts migrating to a wide range of spawning grounds from the wintering area (69° N) in the north to Lista (58° N) in the south (Johannessen et al., 1995). In general spring-spawning herring do not feed for about half a year during the wintering and spawning season (Slotte, 1999b). Thus, energy for gonad development and spawning migration must be obtained from energy stored during the feeding period. This eliminates any influence that unaccounted feeding activity can have on fecundity (Kurita et al., 2003). The whole body energy loss increases two to three times during spawning migration while the relative energy loss decreases with fish size (Slotte, 1999b). Logically, in stationary populations, there is no migration cost on adopted life history strategies. This suggests a different basis of partition between body growth and reproduction compared with migratory populations.

Following this framework, the objective of the present study was to test if differences in life history strategies of migratory and stationary herring populations result in a dissimilar partition between body growth and gonad investment, i.e. fecundity.

2. Materials and methods

2.1. Fish measurements, ovary sampling and related indices

For this study, advanced maturing/prespawning samples were taken at different locations on the Norwegian coast (Fig. 1; Table 1). The migratory Norwegian spring-spawning (NSS) herring were caught in early February 2008 off the Norwegian coast with a pelagic trawl (Egersund trawl, 890 m circumference) during an IMR (Institute of Marine Research, Norway) research cruise with the commercial vessel M/V Libas. Lindåspollene (LP) samples were taken between late January and March prior to the spawning seasons of 2009 and 2010. In this area and during the same period NSS herring were also caught, as demonstrated by otolith analyses (Johannessen et al., 2009), both inside the bay (NSSILP) in 2009 and 2010, and right outside Lindåspollene (NSSOLP) in 2009, close to the Lurefjord. The latter sample was analysed separately from the others because a higher contribution of ‘strange herring’ is expected to occur outside Lindåspollene (Johannessen et al., 2009). Fish from Trondheim fjord (TR) was taken in a branch of the fjord (Åsenfjorden) in March 2010. Herring from Landvikvannet (LV) were collected inside the ‘lake’ in May 2010. All samples from stationary stocks were taken using gill nets by local fishermen. After capture, the herring were processed immediately or kept intact on ice and taken to the laboratory for further processing within maximum 24 h.

For all stocks, individual total length (TL) was measured to the nearest 0.5 cm below and whole body weight (W) was recorded to the nearest gram. In all individuals the gonads were carefully excised and weighed fresh (OW) to the nearest 0.1 g. For each female one sub-sample of ovarian material was collected from the right lobe, immediately fixed in 3.6% phosphate-buffered formaldehyde and stored for at least 14 days before any analysis. The ovary of Atlantic herring is considered to be homogenous in internal structure (Ma et al., 1998). Otoliths were collected from almost all individuals and age and ‘stock type’ were determined based on the otolith appearance by experienced readers. Stock classification and age determination of Atlantic herring based on otolith appearance is a method which was also used by Clausen et al. (2007) and Johannessen et al. (2009). When age or stock origin could not be determined the individual was excluded from the analysis. Eight maturity stages (Mjanger et al., 2007) were discriminated based on macroscopic inspection of the gonads: 1: immature; 2–5: maturing or prespawning; 6: spawning; 7: spent; and 8: resting stage. Following this classification, all females in maturity stage 1, 6, 7 and 8 were excluded from the present fecundity analysis. Somatic condition factor (Ks) and gonadosomatic index (GSIs) were estimated as:

$$Ks = \frac{100 \times (W - OW)}{TL^2 \text{ (no unit)}}$$

GSIs = \[\frac{100 \times OW}{(W - OW)} \text{ (in percentage)}\]

where W is the whole body weight, OW corresponds to gonad weight, and TL the total length.

2.2. Fecundity estimation (whole mount)

Fecundity was estimated by applying the auto-diametric method (Thorsen and Kjesbu, 2001). A portion of each fixed ovarian
sample was analysed and thereafter discarded, the remaining part was saved for further histological analysis (see below). A minimum of 200 developing oocytes were analysed per female using automated image analysis. For each oocyte, the following variables were measured: area, perimeter, ellipse major and minor axis and circularity. Following this operation mean, standard deviation, max, min, and 95% confidence interval (95% CI) were automatically given. The diameter of the leading cohort (LC) was defined as the mean diameter of the largest 10% measured oocytes. Individual fecundity (F) was defined as the number of vitellogenic or hydrating oocytes (i.e. oocytes still trapped within the follicle layer) in the whole ovary and estimated by the equation:

\[
F = 1.708 \times 10^{10} \times (1.04 \times OW^{0.936}) \times OD^{-2.301}
\]

where OD is formalin-fixed mean oocyte diameter (in μm). Since only fresh ovary weight was registered, a correction factor (Kennedy et al., 2011) was added to the original equation (Óskarsson et al., 2002) to correct for the approximate 4% increase

Table 1
Number of individuals (both males and females) sampled in each area and period of time, basic statistics on total length and age, as well as number of females analysed for fecundity and atresia.

<table>
<thead>
<tr>
<th>Geographical Area</th>
<th>Year</th>
<th>Stock</th>
<th>n</th>
<th>Total length (cm)</th>
<th>Age (years)</th>
<th>Analysed females</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>Stationary</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lindåspollene</td>
<td>2009</td>
<td>LP</td>
<td>167</td>
<td>32.4</td>
<td>29.0</td>
<td>35.5</td>
</tr>
<tr>
<td>Lindåspollene</td>
<td>2010</td>
<td>LP</td>
<td>136</td>
<td>32.1</td>
<td>24.5</td>
<td>35.5</td>
</tr>
<tr>
<td>Trondheim fjord</td>
<td>2010</td>
<td>TR</td>
<td>122</td>
<td>27.2</td>
<td>21.5</td>
<td>30.0</td>
</tr>
<tr>
<td>Landvikvannet</td>
<td>2010</td>
<td>LV</td>
<td>223</td>
<td>27.8</td>
<td>22.5</td>
<td>32.5</td>
</tr>
<tr>
<td>Norwegian Sea</td>
<td>2008</td>
<td>NSS</td>
<td>488</td>
<td>32.2</td>
<td>27.0</td>
<td>40.0</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outside Lindåspollene</td>
<td>2009</td>
<td>NSSOLP</td>
<td>140</td>
<td>33.4</td>
<td>28.5</td>
<td>38.0</td>
</tr>
<tr>
<td>Inside Lindåspollene</td>
<td>2009</td>
<td>NSSILP</td>
<td>99</td>
<td>32.3</td>
<td>27.0</td>
<td>37.0</td>
</tr>
<tr>
<td>Inside Lindåspollene</td>
<td>2010</td>
<td>NSSILP</td>
<td>35</td>
<td>32.0</td>
<td>28.5</td>
<td>34.0</td>
</tr>
</tbody>
</table>
in ovary weight due to fixation. The somatic relative fecundity (RFs) was defined as:

\[ RFs = \frac{F}{W - OW} \]

The development in RFs was considered a function of both maturity stage, represented by LC oocyte diameter, and expressions of body metrics (Kurita et al., 2003). To properly contrast the RFs outputs a common LC diameter was selected as a maturity reference point for all populations (see below). This fixed value, found by examination of the plotted maturity data, represented a female at or close to spawning. When defining the threshold value the pattern in atresia was also consulted; the chosen LC diameter referred to a point in gonad growth when RFs apparently stabilised. These normalised settings were also adopted elsewhere when relevant. The modelled RFs were estimated using three values of total length (lower, mid and upper values) in accordance to each population’s size distribution.

2.3. Atresia (histology)

A pre-screening process was undertaken to indicate the levels of atresia throughout ovarian development. As these samples were chosen randomly before the results from the otolith analysis were completed, the final number analysed from each herring population varied somewhat (Table 1). Histological slides were produced in a standard way: the formalin-fixed samples were embedded in Technovit® 7100, and 4-μm thick sections were made and stained with 2% toluidine blue and 1% tetraborate. Atresia was reported using the simple profile method, i.e. the numbers of sectioned normal and alpha stage atretic oocytes (Hunter and Macewicz, 1985) were counted. Thereafter, the relative intensity of atresia, i.e. percentage of oocytes that were atretic was calculated. However, herring atretic oocytes are less likely to be sectioned as they are smaller than normal oocytes. Therefore the relative intensity of atresia was adjusted using principles in Jksesbu et al. (2010) and the following equation (Dunia González, pers. comm.; Kennedy et al., 2011):

\[ RIA = 3.0881 \times A^{0.75} \]

where RIA is the unbiased relative intensity of atresia and A is relative intensity from the present profile counting.

2.4. Historical length-at-age data

Historical length-at-age pooled data were extracted from the IMR central data base (CDB) to establish growth curves for each population (Table 2). Individual body growth (cm/year) was calculated using age-specific mean (historical) total length. For the sake of direct comparison, this analysis was presently limited to age 8, i.e. at a well-established reproductive age with overlapping data from all populations.

2.5. Statistical analyses

The statistics were carried out using Statistica 8.0 (StatSoft, Inc., Tulsa, OK, USA) or Systat® 13 (Systat Software, Inc., Chicago, IL, USA). In case of parametric tests the input data were screened for normality and homogeneity of variance to ensure they did not violate underlying assumptions. Differences among population samples were in many cases tested using one-way ANOVA with a posteriori comparisons (Tukey’s HSD (HSD) test confidence: 95%). ANCOVA was carried out to compare length-at-age information at each geographical location. Traditional correlation or linear or multiple regression analyses were also applied on parts of the presently collated data. IMR CDB body size or age data (>500 specimens per population; Table 2) were contrasted using non-parametric methods, either the Kolmogorov–Smirnov test (two samples) or the Kruskal–Wallis test (multiple samples). The former test was also applied, when appropriate, on present data sets. In every situation differences were considered as significant when \( p < 0.05 \).

3. Results

3.1. Length and age distribution

The fish sampled in this study covered a large range in total length (21.5–40.0 cm) and age (2–20 years old) (Table 1). There were no sex differences in length-at-age within each population (ANOVA; \( p > 0.05 \)); hence further analyses were undertaken on pooled data. Also, the total length distribution did not vary between years, when testable (Kolmogorov–Smirnov test; 2009 vs. 2010: LP herring: \( p = 0.321 \); NSSILP herring: \( p = 0.563 \)). In contrast, the corresponding age varied significantly (by \( \approx 1 \) year) but in an opposite direction for each of these two sympatric populations (Table 1; Kolmogorov–Smirnov test; LP herring: \( p = 0.015 \); NSSILP herring: \( p < 0.001 \)) indicating that ‘stock type’ classifications should be treated with some caution in mixed samples (second author, unpublished results).

The total length- and age distributions clearly differed among the sampled populations (Kruskal–Wallis test; total length: \( p < 0.001 \); age: \( p < 0.001 \)). TR and LV herring generally showed the smallest body size, while LP and LV herring were the oldest and youngest, respectively (Fig. 2). Inside Lindåspollen, LP herring were markedly older than NSSILP herring (2009: \( p < 0.001 \); 2010: \( p < 0.001 \)) but not consistently different in body size (Kolmogorov–Smirnov test; 2009: \( p = 0.011 \); 2010: \( p = 0.747 \)). Herring outside Lindåspollen (NSSOLP herring) were significantly larger but of the same age as the corresponding population inside the pond (NSSILP herring) (Kolmogorov–Smirnov test; 2009: total length: \( p = 0.002 \); age: \( p = 0.074 \)). LP herring were older than TR and LV herring (Kolmogorov–Smirnov test; 2010: \( p < 0.001 \)) but TR herring were markedly closer in age to LP herring than LV herring (Table 1).

3.2. Body growth

The current data on length-at-age fitted generally well with the established historical curves (Fig. 3). No historical data were available for NSSOLP herring. The subsequent Tukey’s HSD test, limited to overlapping age 8 (Fig. 2), showed that the populations were significantly different in growth (\( p < 0.031 \), with one exception (LP vs. LV herring: \( p = 0.972 \)). From an overall perspective, the data could be sorted into three categories: ‘high growth rate’: NSS, NSSOLP and NSSILP herring; ‘moderate growth rate’: LP and LV herring; and ‘low growth rate’: TR herring.
Fig. 2. Age and length distributions (both male and female data included) for each sampling location.

Fig. 3. Mean total length-at-age (both males and female data) for each population. Whiskers represent SD. Historical (H) data are represented by continuous lines.

3.3. Reproductive investment

3.3.1. Atresia

Population-specific prevalence and relative intensity of atresia ($R_{IA}$) were reported and correlated with leading cohort (LC) oocyte diameter. Atresia was present in individuals showing LC oocyte diameters between about 850 and 1250 μm (Fig. 4). Thus, atresia was found throughout the observed range of LC oocyte diameters, except at the largest oocyte sizes (going up to 1400 μm). Only LP and NSS herring were sufficiently represented to do any further data exploration. Within the mentioned ‘atretic window’ the two populations showed a prevalence of 35 and 18%, respectively. Thus, most of these females did not show any atretic oocytes at the time of sampling. There was no significant difference in their total $R_{IA}$ (Kolmogorov–Smirnov test; $p = 0.114$). Restricting the analysis to those females with atresia only, $R_{IA}$ was significantly lower in LP than in NSS herring (Kolmogorov–Smirnov test; $p < 0.001$), corresponding to averages of 5.9 and 7.7%, respectively.
3.3.2. **Fecundity**

In line with the above noted narrow length distributions (Fig. 2), the fecundity data also refer to a limited range in body size, especially for LP, TR and LV where the observed prespawner size varied at most by 5 cm (LP herring: 30–35 cm; TR herring: 25–30 cm; LV herring: 25–30 cm). In the case of the three populations labelled with NSS as prefix, about 80% of the sampled prespawners appeared within a 5-cm range (30–35 cm). The linear regression between relative somatic fecundity (RFs) and total length (TL) was either insignificant ($p > 0.05$) or not robust, i.e., driven by a few extreme values, except for NSS and NSSOLP herring where 7–16% of the variation was explained ($p < 0.001$). There was no evidence of any year effect on RFs (ANCOVA; $p > 0.05$), tested for LP and NSSILP herring.

The further analysis showed that stationary herring produced more vitellogenic oocytes than migratory herring. RFs decreased significantly as LC oocyte diameter increased towards the start of spawning ($p < 0.05$), except in NSS herring where this trend was presently undetectable ($p = 0.108$) (Fig. 5). RFs were a function of TL and LC oocyte diameter, although the overall $p$-value for NSSILP was just insignificant (Table 3). Thereafter, for comparative purposes, the LC oocyte diameter was set constant at 1200 μm across populations (Fig. 5). This prediction revealed that NSS and NSSOLP herring were significantly less fecund than the other populations ($p < 0.001$)
but not significantly different from each other (Tukey's HSD test; 
\( p = 0.983 \)) \((\text{Fig. 6a})\). NSSILP herring showed no significant difference 
when contrasted with LP herring (Tukey's HSD test; \( p = 0.230 \)). TR 
herring presented the highest mean RFs (390 oocytes/g) of all pop-
ulations closely followed by LP and NSSILP herring. In this type of 
analysis, a relative fecundity around 300 oocytes/g appeared to ade-
quately separate migratory and stationary populations, although 
small LV herring deviated by dropping below this crossing line 
\((\text{Fig. 6})\).

### 3.3.3. GSI and K

Implementation of a similar type of calculation exercise as used 
in the previous paragraph meant that the resulting pattern for GSI 
\(\text{(not shown)}\) mirrored the one seen for RFs \((\text{Fig. 6a})\). However, this 
comparison clarified that NSS and NSSOLP herring typically showed 
a prespawning GSI (LC oocyte diameter = 1200 \(\mu\)m) around 20%, 
while LP, LV and NSSILP were at 26%, and TR herring at 30%. In 
the underlying multiple regression analysis, ovary weight (OW) was 
consistently a positive function of both TL and LC oocyte diameter 
\((p < 0.001)\).

The somatic condition factor \((K_s)\) was independent of TL 
\((p > 0.05)\), except for LV herring where \(K_s\) decreased significantly 
with increasing total length \((p = 0.002, r^2 = 0.16)\). Mean \(K_s\) (LC 
oocyte diameter = 1200 \(\mu\)m) clearly varied among populations 
\((\text{Fig. 6b})\); TR\( (0.585)\) and NSS\( (0.616)\) herring showed a significantly 
lower value compared to the other populations \((p < 0.001)\) (HSD 
test). NSSOLP\( (0.665)\), NSSILP\( (0.683)\) and LV\( (0.667)\) herring pre-

cented the highest mean values of \(K_s\) with no significant difference 
among them (Tukey's HSD test; \( p > 0.05 \)). LP herring \((0.660)\) were 

close to NSSOLP and LV herring \((p > 0.05)\) but lower in \(K_s\) compared 
to NSSILP herring (Tukey's HSD test; \( p < 0.05 \)).

### 3.4. Reproductive investment versus body growth

The somatic relative fecundity (RFs) at age 8 of the presently 
studied populations was negatively related to the annual growth 
rate (cm/year) \((p < 0.02; r^2 = 0.763)\). In order to test if this was 
just a local phenomenon in time and space, additional data from 
literature on body growth and relative fecundity from other spring-
spawning herring populations in the North Atlantic as well as data 
from NSS herring caught in 1999 \((\text{Kurita et al., 2003})\) \(\text{(Table 4)}\)

\begin{table}
<table>
<thead>
<tr>
<th>Population</th>
<th>Length-at-age</th>
<th>Fecundity-length</th>
<th>Length-weight</th>
<th>Ovary/somatic weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clyde</td>
<td>(1)</td>
<td>(2)</td>
<td>(1)</td>
<td>(1)</td>
</tr>
<tr>
<td>Rügen</td>
<td>(3)</td>
<td>(4)</td>
<td>(3)</td>
<td>(4)</td>
</tr>
<tr>
<td>NSS</td>
<td>(5)</td>
<td>(6)</td>
<td></td>
<td>(6)</td>
</tr>
<tr>
<td>Eastern part of Gulf of Finland</td>
<td>(7)</td>
<td>(7)</td>
<td>(7)</td>
<td>(8)</td>
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<tr>
<td>Western part of Gulf of Finland</td>
<td>(7)</td>
<td>(7)</td>
<td>(7)</td>
<td>(8)</td>
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<td>Gulf of Riga</td>
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<td>Gulf of St. Lawrence</td>
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\end{table}

**Key to references:** 
(1) Jennings and Beverton (1991); (2) Alnatar and Bailey (1989); (3) Rajasita et al. (2006); (4) Krenkel (1990); (5) Institute of Marine Research (IMR) central database; (6) Kurita et al. (2003); (7) Oyaveye (1983); (8) Laine (1998); (9) Messieh (1976).

were analysed in the same manner \((\text{Fig. 7})\). The results of these 
analyses were also significant \((p < 0.001; r^2 = 0.861)\) suggesting that 
the negative relationship between body growth and reproductive 
investment may commonly be found in spring–spawning herring.

### 4. Discussion

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 repro-
duction in a way that maximises viable offspring \((\text{Roff, 1983; 
Stearns, 1992})\). For Norwegian spring spawning (NSS) herring the 
energy loss during migration is known to decrease with size \((\text{Slotte, 
1999b})\) so, comparatively to a stationary population, it seems more 
advantageous for NSS herring to invest more energy in growth, to 
increase migration potential, and thereby travel large distances to 
the spawning areas. The present results showed that NSS herring 
have higher growth rate and, despite having a bigger body size, pro-
duce significantly less oocytes per gram of body compared to the
stationary populations. This indicates that both the energy allocated to fast growth and migration in NSS herring has a negative effect on fecundity.

The trade-off between body growth and reproduction is among the most important in fishes (Roff, 1983). For migratory NSS it seems advantageous to allocate more energy into growth because metabolic rate decreases with body size (Winberg, 1961) and the optimal swimming speed (velocity at which the total energy expenditure per unit distance travelled is minimal) increases with fish size (Ware, 1978). Therefore, the potential for future reproduction may actually increase in relative terms (i.e. per unit of body mass) but also absolutely as fecundity is clearly a positive function of total length. Tsikiras et al. (2007) also found a negative relationship between body growth rate and fecundity in round Sardinella (Sardinella aurita), although not contrasting intraspecific (population) variance as presently done. Slotte (1999b) concluded that the energy loss for NSS herring during the spawning migration was two to three times higher than during wintering. So a lower relative fecundity could be the consequence of the energy allocated to migration reducing the energy available for egg production (Glebe and Leggett, 1981). A trade-off between migration costs and reproduction was found in the South American characin (Procliodus mariae), where stationary females allocate five times as much energy to egg production as do females that undertake up-river migration (Saldana and Venable, 1983). The great energetic cost of spawning migrations is also well documented for the anadromous American shad (Alosa sapidissima) (Leggett and Carascaden, 1978). Previous studies indicate that there is a general positive association between fecundity and condition of NSS individuals (Öskarsson et al., 2002; Kurita et al., 2003; Kennedy et al., 2011). In this case the studied populations showed markedly different body sizes so a direct comparison of K between them may not be fully appropriate (Cone, 1989). Down-regulation of fecundity by absorption of oocytes through atresia is a known mechanism in Atlantic herring (Öskarsson et al., 2002; Kurita et al., 2003). A full analysis of atresia throughout ovary development was, however, out of the scope of this study. Nevertheless, this analysis allowed us to use a standardised LC oocyte diameter of 1200 μm, i.e., a similar point in the ovary development to properly compare the present reproductive parameters as well as associated body parameters.

The combination of the present results on relative fecundity and the difference in vertebrate counts (Lie et al., 1978) suggest that the “strange” herring caught inside Lindåspollene (NSSOLP) is not composed of true migratory NSS herring. Since Lindåspollene is suggested to be one of many coastal spawning grounds for NSS herring, 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 by Johannessen et al. (2009) who postulated that the migratory component might just return to Lindåspollene to spawn until it has outgrown the stationary resident group (LP). However, looking at the present fecundity results, NSSOLP is more likely to be a migratory component that gradually ceased to migrate out of Lindåspollene and in the long term mixed completely with the resident component. This could explain why this group shows a high and comparable relative fecundity with the stationary ones; similar life style is linked to similar environmental conditions. This was also hypothesised by Johannessen et al. (2009) however their study had no data of fish fecundity. NSS caught outside Lindåspollene (NSSILP) present fast growth rate and a relative fecundity similar to the migratory NSS spawning off the Norwegian coast further north (both NSSOLP and NSS had relative fecundity below 300 oocytes/g). However, the fact that the condition in NSSOLP was higher than in NSS, suggest that NSSOLP may be a component of more semi-stationary (coastal) herring. NSSOLP is likely to be more migratory than LP and conduct inshore and off shore migrations, but still not take part in the large scale oceanic NSS migrations.

In management of herring fisheries, maintenance of stationary populations and a diversity of spawning components are considered to be an important target (Stephenson et al., 1999; McPherson et al., 2001; Bierman et al., 2010; Secor et al., 2009). However, there is currently a lack of knowledge on the genetic diversity of herring populations found along the Norwegian coast. It is hypothesised that the stationary populations analysed in the present study are only a few of many potentially genetically unique populations with phenotypic adaptations to a stationary life in well-defined environments of a wide range of fjords and bays. If this is the case, these stationary populations are direct contributions to the biodiversity along the coast. Moreover, the fact that these populations are maintained in the fjords secure biodiversity also with regard to mammals, birds, fish and other organisms that prey upon the egg, larval, immature and adult stages of herring. As herring are a commercially important species, it is essential to understand the distribution of both genetic and phenotypic diversity as small non-migratory populations are vulnerable to extinction through overfishing. If genetically distinct populations are lost, this represents a decrease in genetic diversity and cannot be replenished through immigration of herring from other areas. Hence, the knowledge gained in the present study on different phenotypic adaptations to stationary and migratory lives suggest that more research effort should be put on studies of stationary inshore resources to improve advice and management governing the latest rules and attempts to maintain biodiversity.

In summary, this study underscores the importance of the species-specific life history adaptations in the reproductive output in populations of Atlantic herring. For NSS herring, body size is an important feature for optimal use of energy for migration. On the other hand, LP and TR herring populations are adapted to a stationary life style where the energy cost of a higher growth rate may be compensated for in such a way. In consequence, migratory species may produce relatively fewer eggs compared with stationary ones. Differences found in NSS, NSSOLP and NSSILP herring populations are a unique example of the high level of adaptability and plasticity observed in herring.

This study supports the findings of Atlantic herring exhibiting a large dynamic range of reproductive strategies which are a reflection of population adaptations to their environment. Future studies should include egg size and quality information to evaluate the female total reproductive investment.

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