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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, Thormøhlensgt. 53 A/B, 5020 Bergen, Norway*
[b] *Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway*
[c] *Møreforsking Marin, P.O. Box 5075, 6021 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

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* Corresponding author. Present address: DTU Aqua, National Institute of Aquatic Resources, Section for Population Ecology and Genetics, Technical University of Denmark, Charlottenlund Slot, Jægersborg Allé 1, 2920 Charlottenlund, Denmark. Tel.: +45 21125086.

E-mail addresses: fdsi@aqua.dtu.dk, filipafgs@gmail.com (F.F.G. Silva), aril.slotte@imr.no (A. Slotte), Arne.Johannessen@bio.uib.no (A. Johannessen), james@mfaa.no (J. Kennedy), olav.kjesbu@imr.no (O.S. Kjesbu).

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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; Geffen, 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, Lindåspollen, 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 Nævdal, 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/Vesterålen 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:

$$\mathrm{Ks} = \frac{100 \times (\mathrm{W} - \mathrm{OW})}{\mathrm{TL}^3(\text{no unit})};$$

$$\mathrm{GSIs} = \frac{100 \times \mathrm{OW}}{(\mathrm{W} - \mathrm{OW})}\ (\text{in percentage}).$$

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