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Evaluation of the frequency of skipped spawning in Norwegian spring-spawning herring

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ABSTRACT

Based upon an under-representation of second time spawners on the spawning grounds between 1935 and 1973, researchers have suggested that Norwegian spring-spawning (NSS) herring (*Clupea harengus*) frequently skip their second spawning event. In order to evaluate this claim with direct evidence, herring were collected over a period of three years from statutory surveys and commercial catches over a wide area covering the feeding, over-wintering and spawning grounds. The development stage of the ovaries was assessed and the intensity of atresia quantified. Only a negligible number of the analysed herring caught were considered likely to skip spawning, thus this phenomenon does not appear to be a common feature of the NSS herring stock at present. In addition, considering the reproductive strategy of herring, it seems doubtful that skipping the second spawning event has ever frequently occurred in this stock.

1. Introduction

Many iteroparous fish do not spawn every year after first maturation. This phenomenon is referred to as 'skipped spawning' (reviewed by Rideout et al. (2005)). Skipping spawning is considered to be a life history strategy which allows increased growth, due to non-participation in spawning, and thereby enhances future reproductive success as a result of a larger body size (Jørgensen et al., 2006). It may also occur when body reserves are so low that the energy expended during spawning would negatively affect survival (Trippel and Harvey, 1989). The frequency of skipped spawning in many fish populations is unknown; it is therefore seldom accounted for in fisheries models (Rideout et al., 2000). Failure to do so may lead to an overestimation of the true number of spawners and thereby the reproductive potential of a given stock (see Yaragina (2010) and references therein). In addition, incorporating skipped spawning could also reduce the variability in current stock-recruitment models (Burton, 1999).

Norwegian spring-spawning (NSS) herring (*Clupea harengus*) is one of the largest commercial fish stocks with an estimated total biomass of 13–14 million tonnes in 2006–2008 (ICES, 2010). These herring undertake an extensive annual migration from the feeding grounds in the Norwegian Sea to their over-wintering areas off north-western Norway and then to their spawning areas off western and south-western Norway (Misund et al., 1997). Analysis of historical data on scale readings taken from herring caught on their spawning grounds between 1935 and 1973 suggested a strong under-representation of second-time spawners (Engelhard and Heino, 2005). Engelhard and Heino (2005) inferred that these fish, which comprised up to 50% of the 2nd time spawners, had deferred the long migration and skipped spawning. The probability of skipped spawning was linked to the size and condition of herring as first-time spawners, and to climatic factors which may have affected food availability (Engelhard and Heino, 2006). However, no additional reports in the peer-reviewed or 'grey' literature described significant numbers of adult herring that would be incapable of spawning at their next spawning opportunity i.e. direct evidence of widespread occurrence of skipped spawning in NSS herring is lacking.

The present study examines maturity data from NSS herring collected over three consecutive spawning seasons in order to test the following alternative hypotheses (H1):

1. Skipping of the second reproductive opportunity commonly occurs in NSS herring
2. Skipping of any reproductive opportunity, after having spawned in a previous year, frequently occurs in NSS herring.

The 2002 year class of NSS herring was exceptionally large and made up a high proportion of the entire stock, at the time of first maturation, in 2006 and then again in 2007 (ICES, 2010). In 2007 and 2008 a substantial part of the 2002 year class should have spawned for the second time, and if predictions of the numbers of skipped spawning herring are correct, then a large proportion of the individuals in the stock should have skipped spawning in both 2007 and 2008, cf. first hypothesis. Substantial numbers of the 1998 and

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1999 year class were also present on the spawning grounds from 2006 to 2008 thus providing a suitable data set for testing the second hypothesis.

As the notion of skipped spawning in herring is based upon the absence of fish from the spawning grounds, they may also be absent from the overwintering grounds (Engelhard and Heino 2005). Therefore, herring were also sampled throughout the feeding area in late summer (July–August). This is approximately three months after ovary development has begun (Kurita et al., 2003). Thus, if herring skip spawning by means of 'resting' i.e. never begin ovary development in that year (Rideout et al., 2005), then they should be detectable at that time of the year.

2. Material and methods

2.1. Collection of samples

Herring were collected throughout the feeding area in July–August 2006 and 2007, the overwintering area in October–November 2006, and most of the known spawning areas in February–March in 2006, 2007 and 2008 during the Institute of Marine Research (IMR) (Norway) research cruises (Table 1; Fig. 1). Female herring were sampled randomly from the catch and each individual was measured (total length, nearest 5 mm), weighed (total, gonad and intestine weight, nearest 1 g) and a sample of scales taken for age determination by experienced age readers at IMR. An ovary sample was preserved in 10% buffered formalin for later laboratory analysis. Fulton's condition factor (K) ($K = 10{,}000 \times \text{total weight}/\text{length}^3$) was calculated for four and five year old fish as these consisted mostly of 1st and 2nd time spawners, respectively.

2.2. Maturity classification

For ovaries containing vitellogenic oocytes, the diameters of 200 vitellogenic follicles were measured using a binocular microscope at 7× magnification, a camera displaying a live image and computer-aided automatic particle analysis. For ovaries which did not contain vitellogenic oocytes, 50 randomly selected pre-vitellogenic oocytes were measured manually using a dissecting microscope and image analysis software.

Previous studies have established that herring oocytes with a diameter <240 μm are pre-vitellogenic, those between 250 and 375 μm are in the cortical alveoli stage and oocytes >375 μm are vitellogenic (Ma et al., 1998; Kurita et al., 2003). We therefore classed fish with a leading cohort (LC) diameter (mean diameter of the largest 10% of the follicles) >250 μm as having begun ovary development in preparation for spawning.

The intensity of atresia was estimated in herring which had a K<0.75 or with oocytes below 1200 μm. These criteria were chosen because atretic intensity is low in herring with a K>0.75 but rises sharply in herring with a condition <0.70, and is absent when oocytes are >1200 μm (Óskarsson et al., 2002). In ovaries where the oocytes were >800 μm, atresia was estimated using whole mount preparations. Atretic oocytes are distinguishable from normal oocytes as they are irregular in shape, relatively smaller than normal oocytes and have an uneven transparency (Óskarsson et al., 2002). A minimum of 200 oocytes were counted and the relative intensity of atresia (percentage of oocytes which were atretic) was calculated. Atresia was estimated in ovaries containing oocytes <800 μm using the profile counting method (Andersen, 2003). A section of the ovary was dehydrated in ethanol and then embedded in Technovit® resin. Several 4 μm sections were then cut and stained with toluidine blue. To prevent the same oocytes being present on different slides, the minimum distance between each section was equal to the LC oocyte diameter. The sections were examined under the microscope with the total number of normal and atretic oocytes counted (atretic oocytes were distinguished from normal oocytes using the criteria from Hunter and Macewicz (1985)) and the relative intensity was calculated. This intensity is an underestimation of the true intensity of atresia as atretic oocytes are smaller than normal oocytes so are less likely to be encountered in histological sections. The true intensity of atresia was calculated using the equation, and iteration, from Kjesbu et al. (2010) where the intensity of atresia in herring (and cod) ovaries was estimated using the profile counting method closely calibrated by the unbiased physical disector method (Andersen, 2003):

$$A_{RIPM} = 0.5379 \times A_{RIDM} + 0.0046 \times (A_{RIDM})^2$$
$$\left(r^2 = 0.975, P<0.001, df = 154\right)$$

A_{RIPM} = Relative intensity of atresia from profile counting
A_{RIDM} = Corrected relative intensity of atresia from disector method

To be considered to be a skipped spawner, a female herring must fit the following criteria:

a) it is or will be a minimum of five years old in the present or coming spawning season (age at first maturation over the last 15 years was rarely below four years (ICES, 2010))
b) The ovaries have one of the following characteristics
   1. The ovaries contain only pre-vitellogenic or cortical alveoli oocytes (cortical alveoli oocyte criteria applies only to herring caught in the overwintering or spawning season).
   2. The LC oocyte diameter is less than 500 μm (applies only to herring caught in the spawning season). Fish with oocytes at this size were considered to be too far behind in development to be able to complete vitellogenesis and spawn in the current spawning season based upon oocyte growth curves (rates) (Óskarsson et al., 2002).
   3. >95% of the oocytes are atretic.

3. Results

The samples used in this study from 2006 to 2008 were dominated by the 1998, 1999 and 2002 year classes (Fig. 2). Four and five year old female fish throughout the study had an average Fulton's condition factor of between 0.64 and 0.73 (Fig. 3). Over 96% of all herring caught in any sampling period were either in the cortical alveoli or vitellogenic stage or in the process of oocyte hydration i.e. ovary development had begun (Table 1). The majority of the fish caught during the summer sampling had an LC oocyte diameter between 350 and 600 μm (Fig. 4). The majority of the fish caught on the overwintering grounds had gonads well developed toward spawning with an LC oocyte diameter in the range of 500 to 1000 μm (Fig. 4). On the spawning grounds, the majority of the females had oocytes in the range of 800 to 1400 μm but there were many with oocytes less than 800 μm (Fig. 4). Only 20 females out of the 1559 herring analysed from the feeding, overwintering or spawning grounds over the three years fitted the criteria indicative of skipping spawning. These consisted of seven 5 year olds (total number of 5 year olds analysed = 285) with the remainder being between 6 and 10 years

Table 1
The location, year of sampling, total number of Norwegian spring-spawning herring sampled (n), length range (mm) and percentage of herring in each gonadal stage. PV = pre-vitellogenic, CA = cortical alveoli, V = vitellogenesis, H = hydrating oocytes.

Location	year	n	Length range	PV	CA	V	H
Feeding area	2006	408	275–400	1.0	2.9	96.1	0.0
Feeding area	2007	204	250–375	3.0	8.3	88.7	0.0
Overwintering area	2006	124	255–385	3.3	0.0	96.7	0.0
Spawning grounds	2006	277	260–380	0.4	0.0	77.3	22.4
Spawning grounds	2007	232	265–380	0.0	0.0	53.1	46.9
Spawning grounds	2008	314	270–400	0.5	0.0	99.5	0.0