Original Article

Female ovarian abnormalities and reproductive failure of autumn-spawning herring (*Clupea harengus membras*) in the Baltic Sea

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Fecundity and reproductive potential are important factors to be considered in evaluating trajectories and demographic predictions of fish populations. Therefore, characterizing the nature and quantifying the extent of any reproductive failure should be considered in fisheries studies. Here, we describe morphological changes in developed ovaries of autumn-spawning herring (*Clupea harengus membras*) caught in the northern Baltic Sea and evaluate the magnitude of this phenomenon during 3 consecutive years. Visibly, abnormal ovaries were histologically characterized by irregular-shaped oocytes in a vitellogenic or final maturation stage with coagulative necrosis and liquefaction of the yolk sphere, degraded follicle membranes, and fibrinous adhesion among oocytes. Such degeneration is presumed to cause complete infertility in the fish. The frequency of fish with abnormal ovaries varied annually between 10 and 15% among all females sampled. However, specific sampling events showed up to 90% females with abnormal gonads. The specific cause of this abnormality remains unknown; however, prevalence was associated with unfavourable environmental conditions encountered before spawning. Thus, ovarian abnormality was positively related to water temperatures, with the highest level found at $\geq 15^\circ$C and negatively related to the frequency of strong winds. The frequency of occurrence of abnormal gonads decreased with the progression of spawning from August to October. The observed abnormality and associated spawning failure will negatively affect the realized fecundity of autumn herring in the Baltic Sea and may act as a limiting factor for recovery of the stock, which has experienced profound depression during the last three decades.

Keywords: Gulf of Riga, hydroclimate, ovarian histology, reproductive disturbance, spawning aggregations.

Introduction

Annual reproductive capacity is a key factor in evaluating trajectories and demographic predictions of fish population dynamics. This, in turn, has direct implications for fisheries management, both in the rebuilding of depleted stocks and in making predictions of potential yields. Therefore, reliable estimates of fish population/stock reproductive potential have a critical role in management, and the extent of reproductive irregularities or failure should be accounted for in fisheries models (e.g. Yaragina, 2010).

Skipped spawning is a phenomenon that may significantly affect the annual reproductive potential for fish populations (Rideout and Tomkiewicz, 2011). This phenomenon has been recorded both for freshwater and for marine fish (Holmgren, 2003; Milton and Chenery, 2005; Loher and Seitz, 2008) and is considered as an adaptive life history strategy that allows increased growth and thereby enhances future reproductive success as a result of a larger body size (Engelhard and Heino, 2005; Jørgensen *et al.*, 2006; Folkvord *et al.*, 2014). Resting and reabsorbing, the most frequent recorded forms of skipped spawning, are commonly associated with dietary deficiencies and poor nutritional condition of females (Rideout *et al.*, 2000, 2006; Kurita *et al.*, 2003; Engelhard and Heino, 2006; Kennedy *et al.*, 2010; Skjæraasen *et al.*, 2012). Three general forms of skipped spawning have been defined for

female fish (Rideout *et al.*, 2005; Rideout and Tomkiewicz, 2011): (i) retaining (oocytes become fully developed and may be ovulated, but are never released); (ii) reabsorbing (oocyte development for the coming spawning season begins, but is interrupted before vitellogenesis is complete, and all developing oocytes are reabsorbed via follicular atresia); and (iii) resting (mature females, i.e. have spawned previously, in which the most advanced oocytes remain in a previtellogenic state throughout the year). However, reports of skipped spawning at a late stage of vitellogenesis are relatively rare in wild-caught marine fish (Rideout *et al.*, 2000, Tomkiewicz *et al.*, 2003), and little is known about underlying causes and mechanisms.

While skipped spawning refers to ephemeral intermittent events, reproductive abnormalities that lead to permanent reproductive failure in fish can be caused by bioaccumulation of toxic substances or exposure to environmental contaminants (Jones and Reynolds, 1997; Lawrence and Hemingway, 2003). Such changes may lead to permanent pathological changes in both female and male fish and result in severe implications on natural populations, including population losses (Bergek *et al.*, 2012). In addition, reproductive disorders may be caused by thermal pollution—effluents of cooling water from nuclear power plants at high temperature (Luksiene and Sandström, 1994). Also, infestations by parasites may severely affect reproductive potential and behaviour of fish (Barber *et al.*, 2000). Because the magnitude of effects vary, reproductive success and related disorders in fish should be incorporated into integrated indicators of ecosystem health (Thain *et al.*, 2008) and ecosystem status assessments in general (Levin *et al.*, 2009).

Atlantic herring (*C. harengus*) is iteroparous, with the female sex representing a determinate fecundity type in which all oocytes to be spawned develop synchronously to be released during a single spawning event (total spawner; Murua and Saborido-Rey, 2003; Lowerre-Barbieri *et al.*, 2011). As a capital spawner, reproductive costs are subsidized from energy reserves such as fat accumulated in muscle tissue. Thus, the amount of resources available significantly influences the individual reproductive strategy in herring, including fecundity determination, fecundity down-regulation, and ultimately skipped spawning (e.g. Kurita *et al.*, 2003; Kennedy *et al.*, 2010; Bucholtz *et al.*, 2013). Furthermore, different Atlantic herring populations have contrasting spawning strategies relative to spawning season and spawning habitats (Iles, 1964).

In the Baltic Sea, two races, spring and autumn spawners, have been distinguished (Heincke, 1898). In contrast to the spring-spawning herring that has successfully adapted to the variable environmental conditions of the Baltic Sea driven by its estuarine circulation, autumn spawners find favourable conditions only during periods of relatively warm winters and high salinity (Kalejs and Ojaveer, 1989). Thus, autumn spawners might be unable to reproduce every year in the northernmost parts of Baltic Sea, i.e. the Gulf of Finland and Bothnian Sea, which has low salinity and is ice covered in winter (Ojaveer and Kalejs, 2005). However, autumn spawners were strongly dominant in herring catches in the Baltic Sea about a century ago (Hessle, 1931 and references therein). Spring and autumn herring are not managed as distinct fish stocks in the Baltic Sea (ICES, 2014), and information over the years on the proportion of autumn spawners in the herring populations and catches does not exist. However, current very low catches in the gillnet fishery, the gear typically used for autumn-spawning herring, indicate that the share of autumn spawners is now negligible in Baltic Sea herring.

The present study focuses on the reproductive performance of the autumn-spawning herring in the Gulf of Riga, northeast Baltic Sea, particularly recently observed ovarian abnormalities. The reproductive ecology of this fish was extensively investigated in the 1950s and 1960s. These historical observations suggest that the main spawning areas for the autumn herring in the northeast Baltic Sea are located in the Gulf of Riga. The fish mature at 3−4 years of age and begin spawning in the second half of August at slopes of 10−15 m depth, where suitable water temperatures exist. Mass spawning occurs at a relatively narrow temperature range (12−16°C). Spawning extends until mid-November and covers a relatively wide depth range (Ojaveer, 1970). We have recently revitalized investigations of this currently depressed and data-poor fish in the Gulf of Riga (Arula *et al.*, 2012) to obtain information on population status as well as on reproductive performance of individual fish to shed light on the reasons responsible for the depression.

In the present study, we sampled autumn-spawning herring in two spawning areas in the Gulf of Riga for determination of sex and maturation stage. We applied histological techniques to characterize ovarian abnormalities in the late maturation/early spawning stage causing retention of eggs and used macroscopic investigations to quantify the magnitude of the phenomenon during 3 consecutive years (2011−2013). The specific aims of the study were to: (i) identify and describe histological characteristics of abnormal ovaries and evaluate the nature of the phenomenon; (ii) quantify the magnitude and spatio-temporal dynamics of this abnormality; and (iii) investigate and identify the significant factors associated with the phenomenon.

Material and methods

Fieldwork and data

Herring were collected from both commercial and experimental catches with gillnets in two spawning areas in the Gulf of Riga (Baltic Sea) near Kihnu Island and at the southern coast of Saaremaa (Figure 1). Sampling was performed in 3 consecutive years (2011−2013) throughout the entire spawning season from mid-August to the end October (18 samples in 2011, 19 in 2012, and 13 in 2013). The autumn herring from the northeastern Baltic Proper spawn at the coast of Saaremaa Island, whereas the Gulf of Riga autumn herring utilize spawning areas around Kihnu Island (Ojaveer, 1970). From each of the 50 samples, ca. 100 individuals were sampled for routine biological analysis, i.e. total length and total weight were recorded and otoliths were obtained for age determination. Sex was determined and maturation stage assessed on a maturity scale developed for herring (ICES, 2011). The scale includes six stages: I. Immature, II. Maturing, III. Spawning, IV. Spent, V. Regeneration (including skip of spawning), and VI, Abnormal, several with substages. Of the total of 4835 herring investigated, 2172 were autumn-spawning males and 2477 were 3- to 8-year-old autumn-spawning females (Figure 1).

Fulton's condition factor, *K*, was calculated as:

$$K = 100 \times \frac{TW}{TL^3}, \tag{1}$$

where *TW* is the total weight (g) and *TL* is the total length (cm) of the fish.

Water temperature was recorded by a self-contained medium-range (600 MHz) oceanographic upwards-facing, bottom-mounted recording Doppler current profiler manufactured by Aanderaa Data Instruments with hourly resolution from August to October in 2013. As the water temperature was strongly
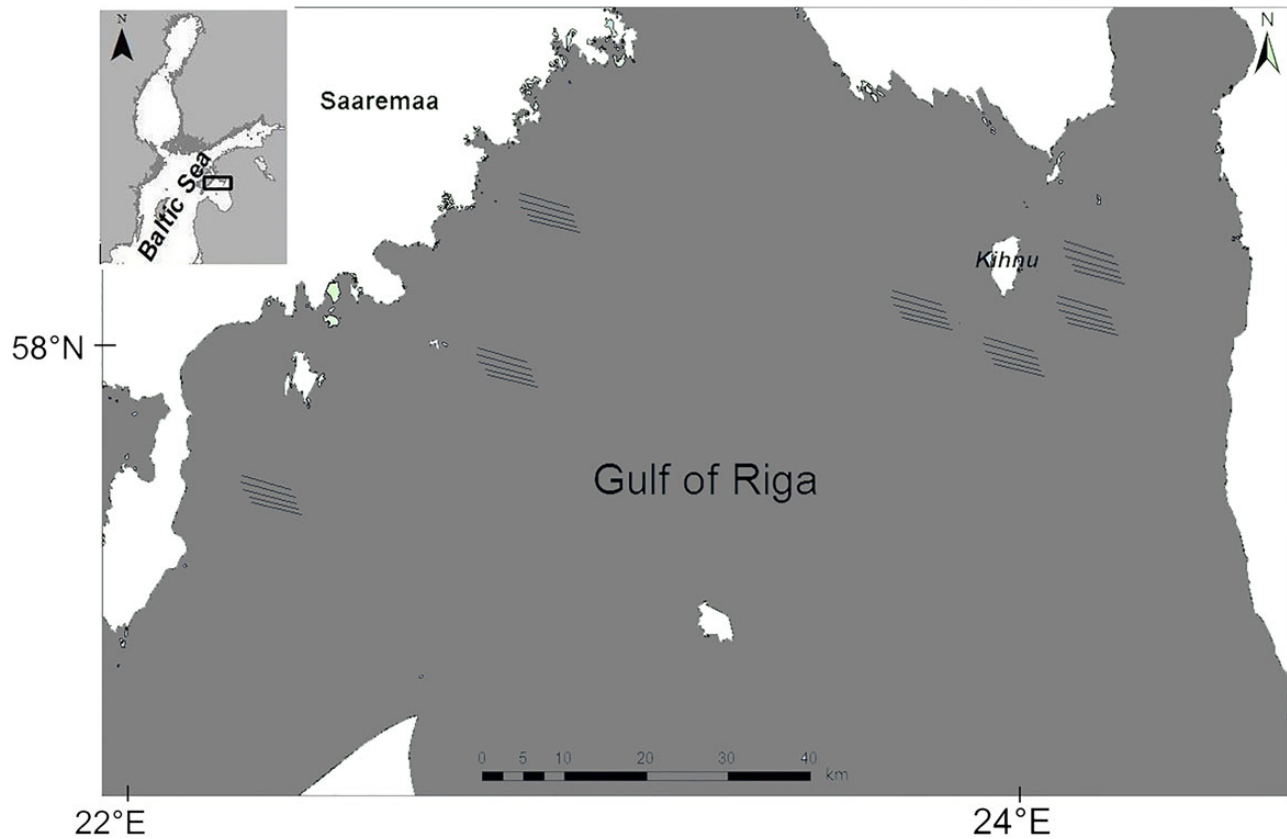
Figure 1. Sampling locations of autumn herring in the Gulf of Riga (Baltic Sea). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

coupled ($r^2 > 0.95$) with air temperature measured at the nearby meteorological station, we used the air–water temperature regression to calculate water temperatures for all 3 years. Windspeed (the maximum value during the 2 weeks before fish sampling) was used as a proxy for the water column instability and physical disturbance. Air temperature and windspeed data were provided by the Estonian Environmental Agency.

Histological analysis

Fresh ovaries from five females with signs of abnormality and one normal ovary were sampled for histological analyses of development. Ovaries from the dissected females were photographed and preserved in formalin buffered with $NaH_2PO_4 \cdot H_2O$ and $Na_2HPO_4 \cdot 2H_2O$. In the laboratory, a cross section of tissue was dissected from the centre of the right ovary lap. The ovarian tissue samples were dehydrated in ethanol and xylene using standard procedures, embedded in paraffin, cut into 4-μm sections, and stained with haematoxylin and eosin (H&E). Photomicrographs at different magnifications ($\times 20$ and 40) were obtained from histological sections using an Olympus digital camera (DP71) and used to describe ovarian characteristics.

Statistical analyses

The percentage of females with ovarian abnormalities was calculated by month, area, and age class. Normal specimens of herring included in the analysis were characterized as "spawning prepared", Stage IIIa (ICES, 2011). Fish in this stage possess ovaries with clearly visible, hydrated oocytes, but are not running or have hydrated

oocytes in their terminal oviduct. Ovaries fill most of the body cavity. Their colour ranges from translucent to mother of pearl. Abnormal specimens were characterized as "abnormal" in the late maturation/early spawning stage (Stage VI; ICES, 2011). Effects of water temperature, turbulence, and body condition on the probability of developing ovarian abnormalities were assessed with generalized linear model (logistic regression) in the R statistical software. The response variable was the presence/absence of ovarian abnormalities (binary, "1" for abnormal ovary Stage VI, "0" for healthy specimen, Stage IIIa). Explanatory variables in individual models were the condition of the specimen, sea surface temperature, maximum windspeed during the previous 2 weeks, and their interaction with age class of specimens and month in two spawning areas. Yearly differences in the rate of abnormality were assessed for both areas together with monthly and regionally balanced bootstrapping, i.e. by testing for interannual variation repeatedly ($n = 999$) from spatio-temporally balanced subsamples.

Results

Macroscopic abnormality and histological diagnosis

Macroscopic characteristics of normal and abnormal development of sampled herring ovaries are illustrated in Figure 2. The ovary is covered by a membrane (tunica) from which transverse bands (septa) of connective tissue subdivide the ovary into sections, giving it a lamellar structure. While this lamellar structure is seen in early maturation stages as transverse grooves, they are no longer visible in the late vitellogenic stage that is characterized by distinct yolked and opaque oocytes in the significantly expanded ovary (Figure 2a and b). The gross morphology of the abnormal ovaries
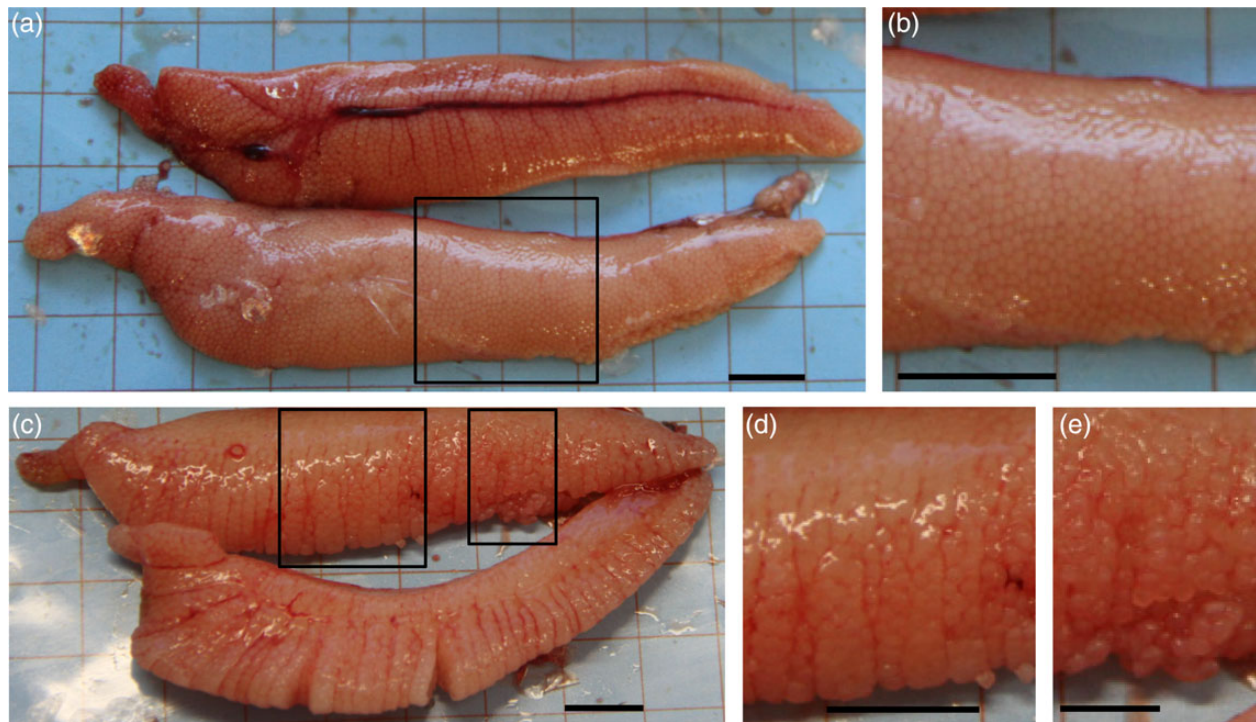
Figure 2. Photographs of normal (a and b) and abnormal (c and e) ovaries of female herring (*C. harengus*) in a late vitellogenic stage, dissected from wild-caught fish. Total length, body weight, and ovary weight of fish with normal and abnormal ovaries: 20.2 cm, 67.6 g, 16.2 g, and 17.3 cm, 72.2 g, 17.5 g, respectively. Black square in (a) indicates the area enlarged in (b), and squares in (c) indicate the areas enlarged in (d) and (e), respectively. Scale bar = 1 cm.

in late vitellogenic of the final maturation stage differed from normal ovaries in two ways (Figure 2c and e). The ovarian structure had deteriorated, and deep grooves in the tunica were apparent, possibly related to the transverse bands of connective tissue (Figure 2c). In addition, the developed oocytes appeared blurred and clustered (Figure 2d and e).

The normally developed ovaries were dominated by oocytes in the late vitellogenic stage that is characterized by the follicular layer of the developing oocytes being completely formed as well as by profound incorporation of yolk (Figure 3a and c). In the regular-shaped late vitellogenic oocytes, spherical yolk globules, stained intensely pink, fill the entire cytoplasm, whereas clear cortical alveoli are found in a narrow band in the periphery of the cell. Among the vitellogenic oocytes, purple-stained primary growth oocytes are visible. In comparison, the abnormal ovaries were dominated by irregular-shaped oocytes in the vitellogenic yolk stage or in final maturation characterized by coagulative necrosis and liquefaction of the yolk sphere in the oocytes, and degenerated oocyte membranes (Figure 3b and d). Furthermore, fibrosis caused pronounced adhesion of oocytes. Thus, the typical ovarian structure was greatly affected, and the entire ovary had lost its normal architecture.

Spatio-temporal pattern of the occurrence of ovarian abnormalities

Of the 2477 females 3–8 years old that were inspected, 327 had abnormal gonads (13%). The within-sample proportion of ovarian abnormality was highest in catches from the Saaremaa spawning area in August (Figure 4; *f*-statistic between the six groups was 2.855 on 5 and 44 d.f., $p = 0.03$). Altogether, 228 out of a total of 1073 ovaries were identified as abnormal in the Saaremaa area

(137 of 366 individuals inspected in August, 79 of 549 in September, and 12 of 158 in October), compared with 99 out of 1404 cases in Kihnu (8 of 143 in August, 52 of 922 in September, and 39 of 339 in October).

Bootstrapping ($n = 999$) that balanced for interannual variation in sampling frequency between sites and months indicated that mean levels of the occurrence of gonadal abnormalities varied up to 1.5-fold within years (mean values of 13, 10, and 15% were recorded for 2011, 2012, and 2013, respectively). However, individual sampling events (which consisted of ca. 100 herring each) showed up to 90% females with abnormal ovaries.

In the Kihnu area, the rate of ovarian abnormalities was higher among younger individuals in all months (Figure 5), whereas in the Saaremaa region, the rate either increased (Figure 5a and b) or remained unchanged with age of the fish (Figure 5c). Logistic regressions revealed that the probability of ovarian abnormalities is higher in fish with higher condition in the Kihnu area (slope parameter = 18.622, $p = 1.29e^{-14}$, Figure 6a), despite age class or month of observation, as the parameter estimates for the body condition were the same for all age classes and months; whereas in Saaremaa, occurrence of the phenomenon is unrelated to the body condition of individuals (Figure 4b, slope parameter = -1.4, $p = 0.123$).

Relation to the hydroclimatic environment

When excluding interactions with region or month, ovarian abnormality was positively related to water temperatures (slope parameter = 0.21, $p = 1.4e^{-7}$), which is expected because the highest frequency of ovarian abnormalities was found in August, when the water temperatures are highest. Adding the interaction with spawning area in the model, however, revealed that ovarian
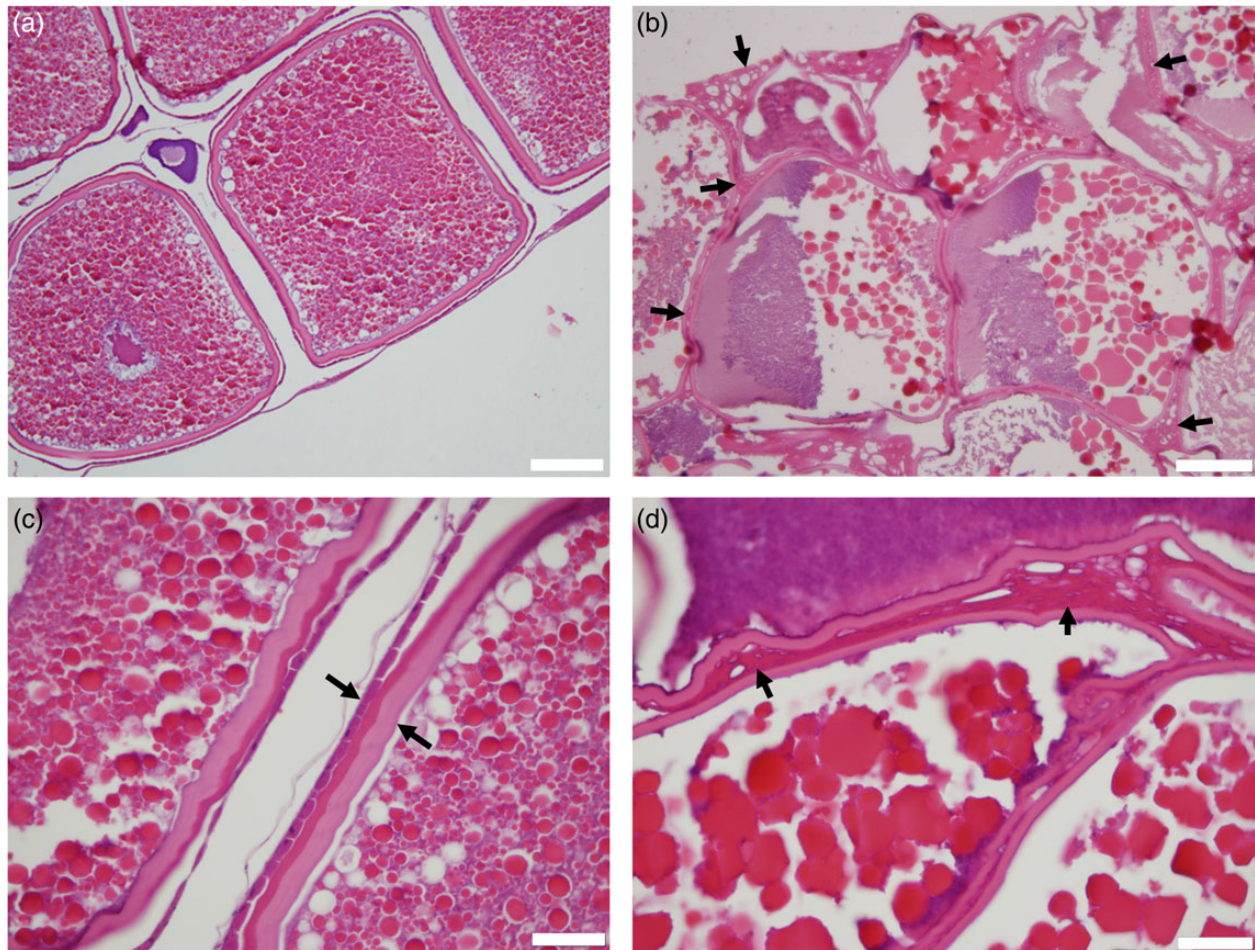
Figure 3. Microphotographs of histological sections of normal (a and c) and abnormal (b and d) ovaries of herring (*C. harengus*). (a) Normal late vitellogenic oocytes of herring filled with yolk globules and peripheral cortical alveoli; small primary growth oocyte, and thin tunica covering the ovary. (b) Degenerated vitellogenic or late final maturation oocytes with coagulative necrosis and liquefaction of the yolk sphere, degenerated follicle membranes and tunica, arrows indicate fibrotic tissue causing adhesion among oocytes. (c) Normal follicular membrane complex of developed vitellogenic oocytes, arrows indicate the cells and chorion. (d) Degenerated follicular membranes and fibronous adhesion (arrows). H&E staining. Scale bars (a) and (b), 200 μm; (c), 100 μm; and (d), 50 μm.

abnormality was related to water temperature only in the Saaremaa area (with the slope of 0.31 and $p = 4e^{-7}$, Figure 7). The effect of maximum windspeed during the 2-week period before sampling was significantly related to ovarian abnormality in the Saaremaa area, but the relationship was negative, with slope parameters -0.26, -0.39, and -0.35, and all $p < 0.0001$ in August, September, and October, respectively, implying that the rate of encountering abnormal individuals decreased with increasing storminess.

Discussion

Reproductive potential and success are key processes influencing demography of fish populations. In fisheries management, it is often taken for granted that once a fish reaches maturity, it spawns every spawning season; however, evidence is increasing that this may not be the case (Rideout *et al.*, 2005; Lowerre-Barbieri *et al.*, 2011; Skjæraasen *et al.*, 2012). The current study confirms that females of one of the most abundant short-living fish species globally—herring—can exhibit gonadal abnormalities that impair its reproductive performance. Although vitellogenesis proceeded to a late stage of ovarian development, oocytes were abnormal and degraded. The morphological structure of herring ovaries was

affected to such a degree that the organ had lost its normal architecture. Furthermore, the fibrinous adhesion among oocytes prevented ovulated eggs from travelling to the edges of the ovarian septa that, in herring, are free leading into the oviduct located along the dorsal side of the ovary. This will impair egg release and result in reproductive failure, which may be of a permanent nature. Although the overall level of the reproductive disorder may be not very high at the annual scale, it may reach up to 61% at certain times in particular spawning areas. As the phenomenon was observed across all studied spawning areas and all 3 years investigated, we conclude that it is a prevalent phenomenon affecting the autumn herring in the Baltic Sea by involving both the open sea and Gulf herring populations. While the intermittent phenomenon of skipped spawning has been hypothesized to be an adaptive life history strategy increasing lifetime reproductive success (Engelhard and Heino, 2005; Jørgensen *et al.*, 2006; Folkvord *et al.*, 2014), results of the present study confirm reproductive disturbances at a late stage of oocyte development possibly due to environmental stress that cannot be considered as adaptive of nature.

Herring is a capital spawner with determinate fecundity—all oocytes to be spawned are recruited early in the reproductive cycle

(Murua and Saborido-Rey, 2003; Lowerre-Barbieri *et al.*, 2011), and numbers of developing oocytes are adjusted through down-regulation, i.e. atresia, as maturation proceeds (Ma *et al.*, 1998; Oskarsson *et al.*, 2002). In extreme cases, herring can skip a spawning season (Bucholtz *et al.*, 2013). Non-reproducing fish have been reported in spring-spawning herring in the Baltic Sea (Bucholtz *et al.*, 2013) and the Norwegian Sea (Oskarsson *et al.*, 2002; Engelhard and Heino, 2005). However, the current study identifies a phenomenon that differs from these descriptions of skipped spawning or infertility. All analysed specimens exhibited atretic oocytes with abnormal appearance, including coagulative necrosis and liquefaction of the yolk sphere, degenerated follicle membranes, and fibrosis causing adhesion of oocytes. The distortion affected the entire ovary, and the degeneration of the ovarian tissues caused rupture of the tunica. Polder (1961) claimed that reabsorption of atretic oocytes in herring was brought about by degeneration of

the membranes followed by active phagocytosis, whereas Bowers and Holliday (1961) claimed, for the same species, that a process of autolysis was responsible. Degeneration of oocytes in the analysed specimens may be due to such processes; however, the fibrinous adhesion and rupture of the tunica probably lead to permanent impairment of reproductive performance. The observed abnormalities in the present study may relate to physiological stress and/or lack of external cues under unfavourable hydroclimatic conditions (see also below). However, other factors, both singular and interactive effects, which have previously been reported to cause reproductive disorders, may also be involved, including exposure to environmental contaminants, bioaccumulation of toxic compounds, and parasite infestations (Breitholtz *et al.*, 2001; Jobling and Tyler, 2003; Schiedek *et al.*, 2007).

Only a few marine fish species have adapted to the spatially variable environment of the brackish Baltic Sea. One such species facing spatial limitations for reproduction is the autumn herring, because this fish is unable to spawn in the northernmost areas due to unfavourable hydroclimatic conditions (Ojaveer and Kalejs, 2005). Thus, the gonadal abnormality observed in the current study may be associated with overall poor adaptation of the fish to local habitat at the border of its distribution area. It is known that autumn herring start spawning at the upper temperature limit in late summer and continue spawning until late autumn. As a typical representative of species with high ecological constraints for spawning-site selection (Ciannelli *et al.*, 2015), autumn-spawning herring require a very narrow temperature range for successful spawning and specific benthic habitat—sand and gravel—to deposit its eggs (Ojaveer, 1970).

Suitable thermal conditions for spawning can initially be found at the uppermost part of the coastal slope in late August (Ojaveer, 1970). Owing to rapid cooling and higher instability of the water column (because of winds) towards autumn, the volume of suitable water masses for spawning increases along with a progression of the spawning season. In herring, ovulated eggs can be retained for at least 7 d before spawning, probably maintained at this time by secretions of the oviduct (Holliday, 1960). If herring do not find suitable thermal habitat for spawning within this time-window, ovarian abnormalities may occur. In the present case, the abnormality
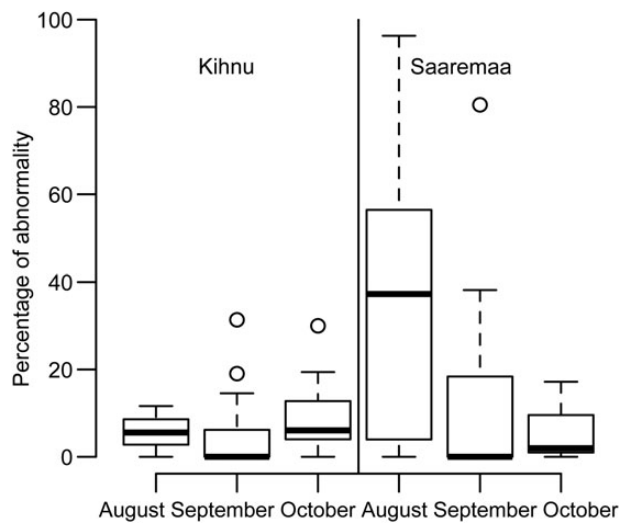
Figure 4. Within-sample percentage of females with abnormal gonads in two spawning areas (Kihnu and Saaremaa) and 3 months (August, September, and October) in the Gulf of Riga during 2011–2013.
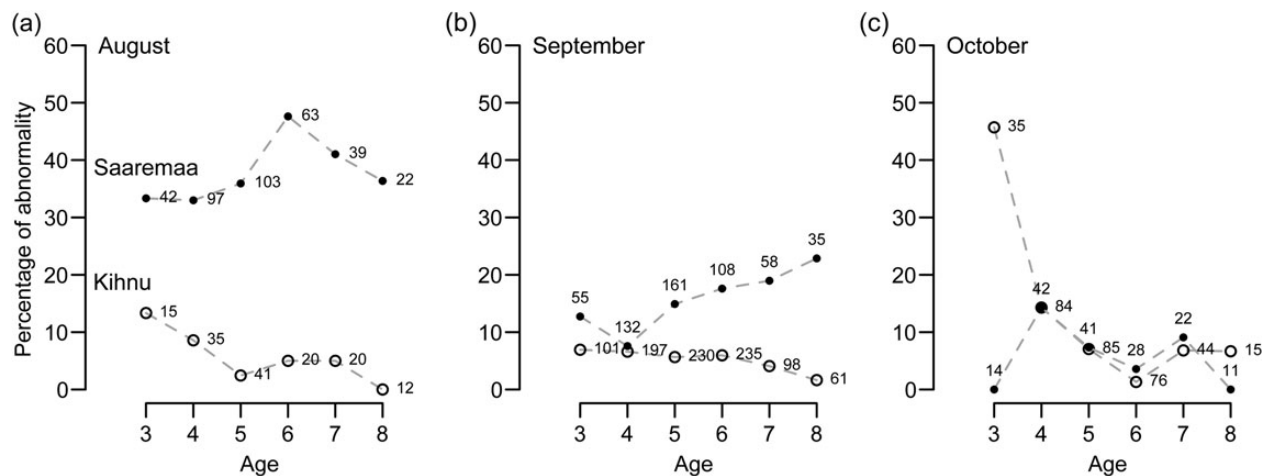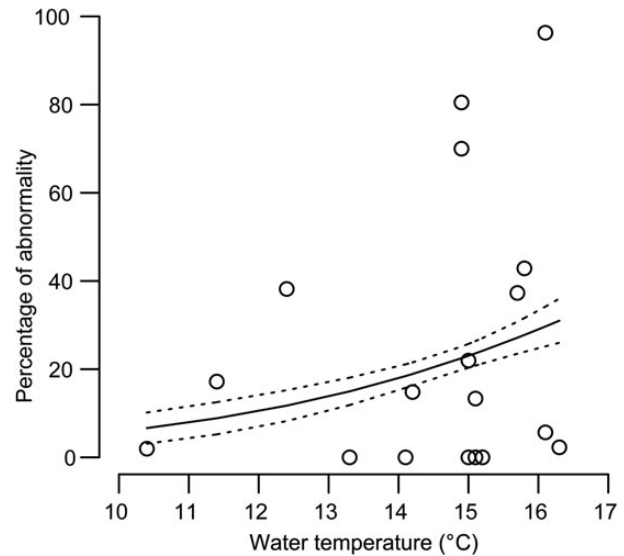

Figure 5. Percentage of abnormality within the age groups of 3–8 years. Filled circles denote data from the Saaremaa area, and empty circles from Kihnu. Small numbers close to each point denote the number of individuals inspected. In (b) and (c), where the points overlap, values for the Saaremaa region are placed above, and values from the Kihnu region to the right side of the point.
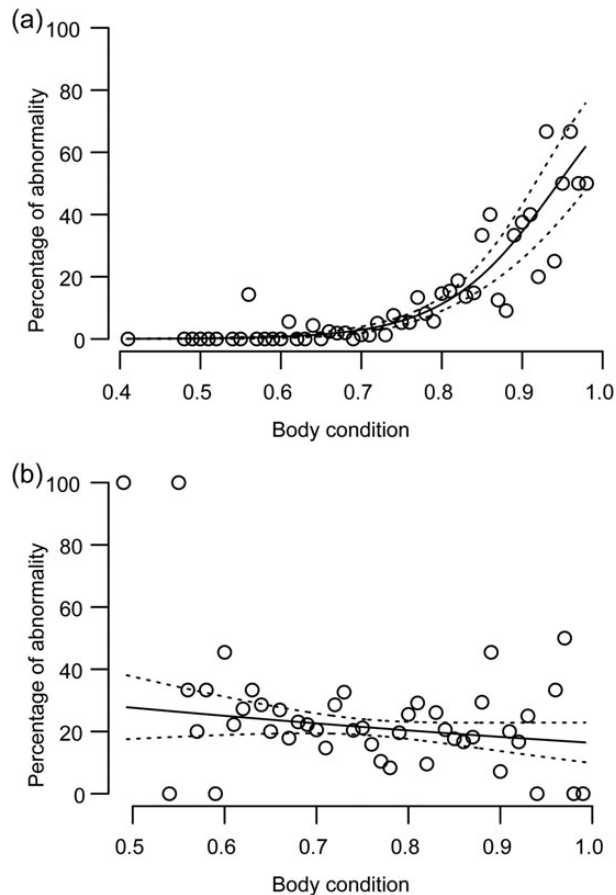
Figure 6. Probability of ovarian abnormality in relation to body condition of individuals in the Kihnu (a) and Saaremaa (b) spawning areas predicted from logistic regression parameter estimates. Points represent percentages of individuals with abnormal gonads at discrete condition value classes (rounded to two digits, 51 values between 0.5 and 1).

Figure 7. Relation between occurrence of abnormal ovaries and water temperature in the Saaremaa spawning area. Points indicate the percentage of abnormal ovaries per sample, line is the logistic regression fit using data of individual specimens ($n = 1073$, slope parameter $= 0.31$, $p = 4e^{-7}$).

occurred before ovulation, possibly because of the lack of external cues. Our results showed a relationship between the frequency of occurrence of reproductive failure and water temperature, which was particularly high early in the spawning season coinciding with high water temperatures (generally $\geq 15°$C). Also, the occurrence of females possessing gonadal abnormality decreased with increased storminess, which might point to increased wind-induced vertical mixing resulting in a larger volume of water with suitable thermal conditions for normal ovarian development. Thus, we suggest that unfavourable hydroclimatic conditions are involved in the observed reproductive disturbance in female herring. This suggestion is consistent with a broader statement that ovarian abnormalities are common for fish that are subjected to unfavourable environmental conditions, including an inadequate temperature regime (Pavlov et al., 2004; Engelhard and Heino, 2006) and specifically hypothesized earlier for flatfish (Fedorov, 1971).

Insufficient food resources and related poor nutritional status have been associated with gonadal atresia and skipped spawning (Kennedy et al., 2010). However, our results clearly show that a higher incidence of gonadal abnormalities was not related to low body condition of the fish. To the contrary, a strong positive relationship was observed between ovarian abnormality and body conditions in the Kihnu area, probably due to a higher frequency of

abnormalities at a late stage of ovarian development when fish condition factors are high. Thus, low energy content and, therefore, poor nutritional status of the fish seems not to be the reason behind the observed gonadal abnormality in autumn herring in the Baltic Sea. Furthermore, although the study area (Gulf of Riga and northern Baltic Proper) is characterized by high eutrophication (HELCOM, 2010), there are no direct industrial pollution sources affecting the area, and the level of pollution and its effects on fish in the area are, in general, moderate (HELCOM, 2010; Ojaveer and Eero, 2011). Furthermore, the occurrence of these abnormalities did not, in general, increase with fish age (Figure 5b). Thus, although contribution from pollution on herring gonadal abnormalities cannot be totally excluded, there is no obvious evidence to suggest such a link.

The major spatial difference observed in several measured parameters in the two spawning areas (i.e. frequency of occurrence of the ovarian abnormality, relation of the phenomenon to hydroclimatic and fish parameters) may be related to the different origins of the herring. Existing information, although originating decades earlier, suggests that autumn-spawning herring originating in the northeast Baltic Proper spawn mainly along the southern coast of Saaremaa Island, whereas the local Gulf of Riga autumn herring utilize spawning areas around Kihnu Island (Ojaveer, 1970). If this is still the case (and in the conditions of substantially changed environment and reduced autumn herring abundance), the open-sea autumn herring seems to face substantially higher reproductive problems in the Gulf of Riga than the local herring population. This might be related, among others, to timing of the start of the spawning migration (resulting in fish finding an unfavourable environment in spawning areas) or to fish facing unfavourable short-term hydroclimatic conditions during the migration route from the open sea into the Gulf of Riga.

Autumn-spawning herring made a substantial contribution to herring landings in the Swedish Baltic Sea fishery about a century ago (up to 90%) and in the former Soviet Union fishery in the

Gulf of Riga until the mid-1970s (up to 47%; Hessle, 1931; Ojaveer, 2003). However, stock abundance has subsequently decreased sharply and has not yet recovered. In the northern Baltic Sea at the border of its distribution area, autumn herring find favourable conditions during periods of relatively warm winters and high salinity with abundant year classes being formed only after mild winters (Kalejs and Ojaveer, 1989). Therefore, in general, autumn herring should benefit from warmer climate. However, the current study demonstrated that higher sea temperature in late summer might be responsible for reproduction disorders of female herring. While excessive fishing pressure historically might have reduced stock abundance, increased summer sea temperatures may function as an additional restraint to recovery.

Findings of the current study have important implications for fisheries management. Gulf of Riga herring are currently managed as a single stock (ICES, 2014), which includes both spring and autumn spawners, with strong domination by spring herring. As evidenced from the current study, autumn herring exhibit reproductive failures, which were not recorded for the local spring herring population (Raid *et al.*, 2010). Furthermore, it is yet unclear what will happen with females with gonadal abnormalities. While there is some limited evidence from the past to suggest that these females might survive, based on findings of hardened residual eggs among developing follicles in female ovaries (Ojaveer, 1970), the widespread and severe distortion of the ovarian tissue in females analysed in this study may result in increased female mortality. Therefore, natural mortality of the autumn herring is relatively high compared with spring spawners. Alternatively, even if the females survive, the phenomenon is presumed to lead to permanent impairment of reproduction. Taken together, the observed reproductive disorder may be at least partly responsible for the currently low abundance of autumn herring in the Baltic Sea, and we recommend that this reproductive failure should be considered in managing this resource, and that autumn-spawning herring should be managed as a distinct unit in the future.

In conclusion, the current study documents a phenomenon of reproductive failure that, in addition to skipped spawning, can influence the reproductive capacity of a fish stock.

Acknowledgements

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