Thermal stratification influences maturation and timing of spawning in a local herring population

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Maturation and timing of spawning in relation to temperature was studied in a local Atlantic herring *Clupea harengus* population at the west coast of Norway inhabiting a small landlocked fjord (7 km^2) separated from the larger outer fjord system by narrow sills. Ambient temperatures varied annually by up to 4°C during both the pre-spawning and spawning periods in February-April, but without affecting the spawning time. Instead, the timing of spawning was found to be strongly related to thermal stratification in response to rapid spring warming, which occurred at about the same time every year regardless of initial temperatures.

Key words: *Clupea harengus*; maturity; temperature; landlocked fjord.

INTRODUCTION

A relationship between temperature and spawning time has been demonstrated in a wide range of marine species such as cod, *Gadus morhua* (Hutchings & Myers, 1994), capelin, *Mallotus villosus* (Carscadden *et al.,* 1997), mackerel, *Scomber scombrus* (Jansen & Gislason, 2011) sole, *Solea solea* (Fincham *et al.,* 2013), Pacific herring, *Clupea pallasi* (Haegele & Schweigert, 1985), Atlantic herring, *Clupea harengus* (Winters & Wheeler, 1996) including the Norwegian spring-spawning (NSS) herring (Husebø *et al.,* 2009). The studies all report a positive relationship between ambient temperatures and the rate of maturation. Physical processes speed up with temperature, but the relationship has also been explained functionally since increasing temperature normally causes water column stratification in spring providing adequate conditions for phytoplankton blooms and thus enhancing larval survival (Sverdrup, 1953; Pingree *et al.,* 1977; Cushing, 1990; Platt *et al.,* 2003). Timing of water column

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stratification and phytoplankton blooms in oceanic and coastal areas has been shown to be tightly linked to large scale cyclic climate fluctuations like the North Atlantic Oscillation (e.g., Fromentin & Planque, 1996; Irigoien *et al.,* 2000; Ottersen *et al.,* 2001, 2010), although local meteorological conditions such as air temperature and tide may also be important (see Sharples *et al.,* 2006). However, in inshore waters, such as estuaries and landlocked fjords, conditions are less influenced by the larger scale climatic fluctuations. Instead, the local air temperature, freshwater run-off and incoming light during spring are the main factors triggering stratification and blooming (Townsend *et al.,* 1992, 1994; Waniek, 2003; Freund *et al.,* 2006).

Along the Norwegian coast there are a number of small fjords and semi-enclosed marine systems that are characterized by distinct summer stratification and vertical gradients in environmental factors such as salinity, temperature, nutrients and oxygen (Matthews & Heimdal, 1980). One of these systems is Lindåspollene, located on the south-west coast of Norway, comprising three relatively shallow basins (~90 m) separated from each other and from the outer fjord by sills of 3-10 m depth (Fig. 1). The restricted connection, combined with freshwater run-off, affects the hydrography of the system (Lännergren & Skjoldal, 1976). Lindåspollene is less influenced by vertical turbulence than the areas outside, and due to the shallow thresholds to the outside fjord the water masses inside the poll are separated in an upper stratum with high seasonal variability in temperature and salinity and a lower part, from about 20 m depth to the bottom, with rather stable conditions (Aure, 1972; Dahl *et al.,* 1973; Lännergren, 1978; Lännergren & Skjoldal, 1976). In Lindåspollene, there is a well documented herring population, which is regarded as distinct from the oceanic NSS herring because of its deviating growth pattern resulting in a smaller size-at-age (Lie *et al.,* 1978; Johannessen *et al.,* 2009). Despite the significant research effort invested into understanding the special Lindåspollene ecosystem, the timing of spawning of the local herring population is not well understood. In the present study we used data acquired during a five year period to explore whether the timing of herring spawning is influenced by 1) change in ambient temperature and by 2) change in surface stratification experienced during the pre-spawning and spawning period.

MATERIALS AND METHODS

The ambient temperature was monitored at selected sites by means of vertical CTD casts using a SAIV model SD204; (i) in the outer basin, Straumsosen, which has a maximum depth of 60 m, (ii) Fluøy (~40 m), (iii) Gølna (~30 m) and (iv) the deepest basin Spjeldnesosen (~90 m). These four stations were all relatively close to either the documented

overwintering area or spawning area for herring (Fig. 1). In total, 37 CTD casts were carried out from February to April from 2006-2010; 11 at Straumsosen, 6 at Fluøy, 12 at Gølna and 8 at Spjeldnesosen. All CTD casts were deployed from the surface to 5 m above the bottom (only downcast data were processed). Data from 0-2 m were flawed and excluded from further analyses. Data exploration showed little change in temperature at depths below 20 m, but strong dynamics between the upper 2-10 m and lower 11-20 m, so only data from 2-20 m were included and assumed to capture the majority of temporal dynamics in temperature. In order to investigate whether thermal stratification influenced maturity and timing of spawning, two depth strata were defined as 2-10 m and 10-20 m. For easier comparison, measurements from each CTD cast were standardised by subtracting the mean value from 2-20 m.

Herring were sampled in January to April every year using monofilament gillnets; 25 m long by 4 m high, with stretched mesh sizes of 24-36 mm (see Langård *et al.,* submitted for further details). The gillnets were set in 3 series á 3 nets near the surface (max depth 5 m). Nets were set in the afternoon (between 17:00 and 19:00) and hauled the next morning (09:00-12:00). Individual herring were scored for gonad maturity stage according to an 8-point scale (1-2: immature, 3-5: maturing, 6: running/spawning, 7: spent, 8: resting stage) based on macroscopic visual inspection (Mjanger *et al.,* 2011).

All statistics were performed using R version 3.0.0 (R Development Core Team 2013, http://www.rproject.org). Statistical modelling was used to calculate the probability of occurrence of herring in maturity stages 4 to 7 by day of the year (Yearday, YD) in order to interpolate the progression of gonad maturity in periods without gillnet samples. Generalized linear mixed-effects models (GLMMs) with a binomial error term and accounting for random variability due to year were used for calculating the probabilities of fish being within a given maturation stage or not (see Langård *et al.,* submitted for further details about the model).

In order to investigate whether temperature could explain timing of spawning, a proxy for spawning time was defined as the proportion of herring being in either maturity stage 6 or 7 based on the gonad maturity probability model. It was then explored whether this spawning time proxy showed a linear relationship to the average temperature in the dynamic upper depth stratum (2-10 m). A proxy for thermal stratification (Tdiff) was then defined as the temperature in the lower depth stratum (10-20 m) subtracted from the temperature in the upper stratum (2-10 m), and it was explored whether the spawning time proxy showed a linear relationship to Tdiff. Simple linear regression models were applied to investigate relationships.

RESULTS

Mean standardized temperature by depth pooled over all years (2006-2010) and intervals of 10 days showed that the proxy for thermal stratification (Tdiff) shifted from negative for yearday 70-79 to positive for yearday 80-89 (Fig. 2). Around the shift between these two periods, the probability of occurrence of spawners was around 50 % (Fig. 3). The temperature in the upper stratum (2-10 m) showed considerable annual variation during both the early pre-spawning (probability of spawning < 0·1, 2-6°C) and late spawning phase (probability of spawning > 0·7, 4-8°C), but there was no relationship between the proportion of spawners and the mean temperatures recorded in the upper stratum (df =35, R^2 = 0·005, ANOVA, P = 0·680; Fig. 4(a)). On the other hand, there was a strong positive relationship between the proportion of spawners and the thermal stratification proxy (df =35, R^2 = 0·517, ANOVA, P < 0·001; Fig. 4(b)).

DISCUSSION

We show that the timing of spawning of a small landlocked fjord population of herring was related to change in thermal stratification regardless of variable ambient temperatures experienced during the pre-spawning and spawning period.

This result deviates from previous findings that maturation rates and spawning time in herring is tightly linked to the ambient temperatures during the maturation phase (Runnström, 1941; Haegele & Scheigert, 1985; Hay, 1985; Winters & Wheeler, 1996; Husebø *et al.,* 2009; Óskarsson & Taggert 2009). It has been shown previously by Hay (1985) that timing of spawning in local populations of Pacific herring deviate from those of the main population, several of these populations were associated with inlets. He emphasizes that these exceptional cases illustrate that spawning time can be influenced by other factors than the temperature level, such as tides and time of day (Spratt, 1981), local weather conditions and ice break (Tyurnin, 1973; Barton & Wespestad, 1981).

The Lindåspollene fjord system differs considerably from the open oceans in hydrography and timing of plankton blooms and it may be beneficial to adapt timing of spawning to other features than the ambient temperature. Since a phytoplankton bloom not only relies on light for photosynthesis, but also stable surface water to avoid sinking out of the photosynthetic zone (Huisman *et al.,* 2004 and references herein), it may be beneficial for herring to adapt maturation and timing of spawning to the stability of the surface layer rather than ambient temperature. A shift to higher temperature above than below the thermocline is a precise indication of an enduring stability in surface layers leading to the spring plankton

bloom, and the timing of spawning in Lindås herring can be explained as an adaptation to match local plankton bloom and enhance survival of larvae.

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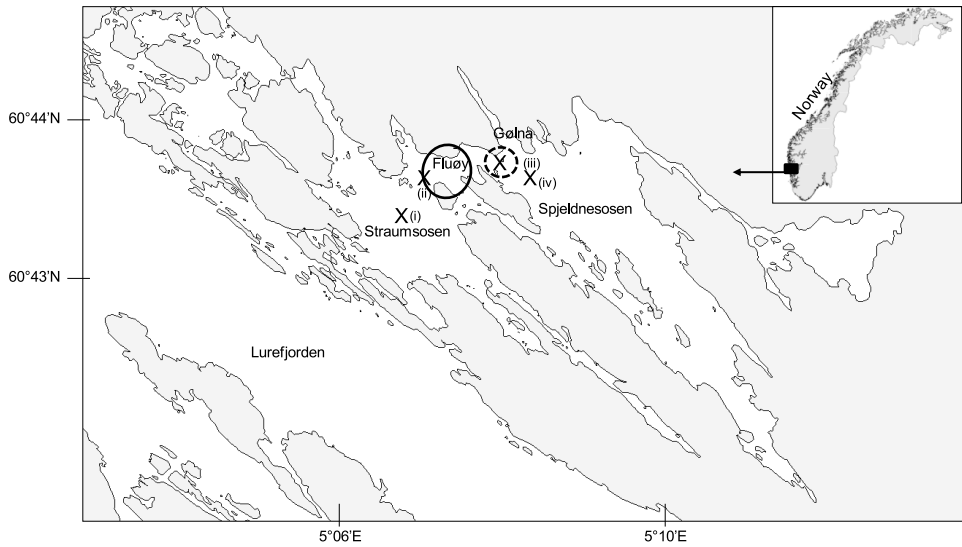
Figures

FIG. 1. Map of Lindåspollene, where X denotes the positions for the CTD stations, open circle denotes the main spawning grounds (2006-2010) and the dotted open circle indicates the overwintering area.
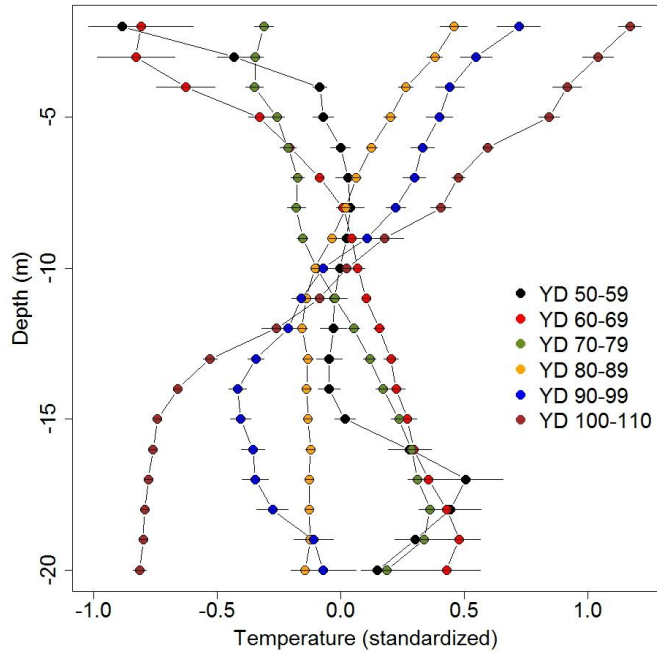
FIG. 2. Standardised temperature at depth averaged over 10 days over all stations and years (mean±SE).
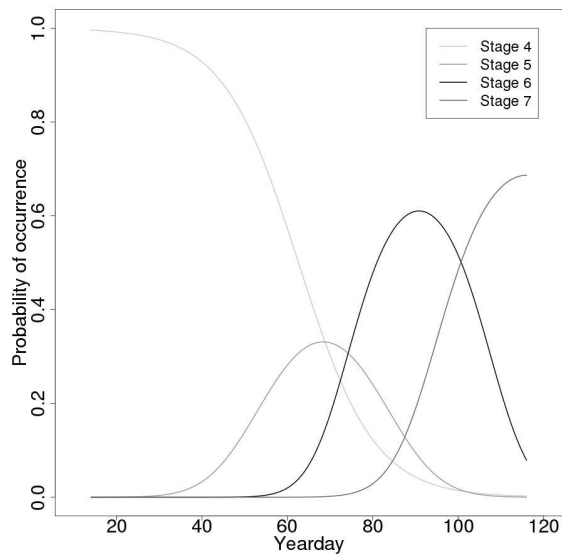

FIG. 3. Maturation model - The lines show the probabilities of finding a given maturation stage of herring depending on yearday (see methods for further details of the model).
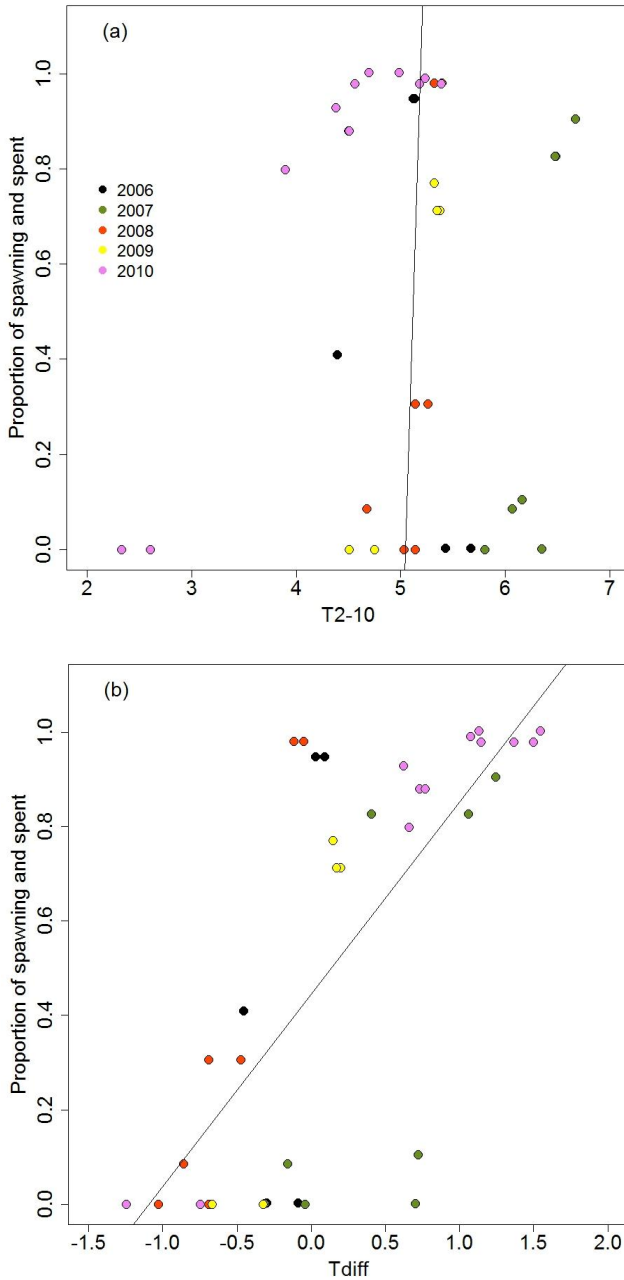
FIG. 4. Proportion of herring in spawning or spent stage (GMI 6-8) as function of (a) mean temperature in the upper depth stratum (2-10 m; T2-10) and (b) mean difference between temperature in the upper (2-10 m) and lower (10-20 m) depth strata (Tdiff). Solid lines indicate the fits from linear regression models.