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Spawning time of Atlantic herring (*Clupea harengus*) populations within a restricted area reflects their otolith growth at the larval stage

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ABSTRACT

Larval growth from three putative populations was estimated by microstructure analysis of otoliths of four year classes of adult herring sampled over a wide spawning season (February-June) in and around an inland brackish water lake (Landvikvannet) in southern Norway during the years 2012–2015. Mean width of daily increments at distances between 20 and 170 µm from the otolith core were significantly higher in Landvik herring (peak spawning in May) compared with the two other populations, Coastal Skagerrak spring spawners (peak spawning in March-April) and Norwegian spring spawning herring (peak spawning in February-March). These population differences were observed for all studied year classes and years and highly consistent with expected temperature dependent larval growth based on timing of successive spawning events. The observed patterns imply that timing of spawning was population specific with a tendency of adult herring to spawn at the same time and under the same conditions as they hatched themselves. This was also supported by vertebral counts, which are negatively correlated with temperatures during the embryonic stage. Firstly, Landvik herring which experienced higher ambient temperature during the embryonic stage were characterised by significantly lower counts than herring from the two other populations. Secondly, daily otolith growth also tended to decrease with increasing vertebral counts within the populations. The present study signifies the importance of otolith growth history for population discrimination in herring, even within the same spawning season, and further supports the use of vertebral counts in the continuous discussion on herring population structure, assessment and management.

1. Introduction

Population structure of Atlantic herring (*Clupea harengus*) is known to be highly complex (Iles and Sinclair, 1982) and it has been frequently studied in recent years (André et al., 2011; Lamichhaney et al., 2012; Johannessen et al., 2014). Genetic studies have revealed low levels of genetic differentiation among populations that have distinct temporal and spatial spawning locations, but mix during feeding migrations (Ruzzante et al., 2006; Gaggiotti et al., 2009; Bekkevold et al., 2015). However, clear genetic differentiations could be demonstrated among Baltic herring (Corander et al., 2013) as well as geographically isolated populations in Norwegian fjords (Pampoulie et al., 2015). Also, there is a plasticity and a high level of adaptability of herring in terms of contrasting behaviour, morphology and life history (McQuinn, 1997; Geffen, 2009). Hence, biological characteristics, like otolith microstructure or shape, can be used as population markers where genetic markers have not detected any differentiations (Mosegaard and Madsen, 1996; Clausen et al., 2007; Libungan et al., 2015b).

Otolith analysis is a powerful tool when analysing population structures of fish because it allows accurate estimates of age and growth of individuals at both the daily and yearly level (Campana and Thorrold, 2001). In marine species with high gene flow such as Atlantic cod (Cardinale et al., 2004), haddock (Begg and Brown, 2000), blue whiting (Mahe et al., 2016), European anchovy (Bacha et al., 2014) and Atlantic herring (Libungan et al., 2015a), otoliths have been used to detect population structures. Phenotypic information as well as experienced environmental changes can be extracted from otoliths (Campana, 1999). The otolith growth can be influenced by several factors such as temperature (Folkvord et al., 2004), prey density (Johannessen et al., 2000) and photoperiod (Mugiya, 1987). Consequently, differences in adult spawning patterns might be exhibited in the otolith microstructure of their larvae (Fitzhugh et al., 1997).

In Atlantic herring, otolith microstructure has been used to identify spring, autumn and winter spawners (Mosegaard and Madsen, 1996; Clausen et al., 2007). Otolith analysis is also used to separate mixing herring in the Skagerrak region for management and assessment purposes (ICES, 2016). Several studies on population dynamics of herring have used otolith microstructure analysis, but most studies

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have used otoliths of herring with distinct spawning seasons (Brophy and Danilowicz, 2002; Husebø et al., 2005; Brophy et al., 2006).

Within a restricted area in and around an inland brackish water lake (Landvikvannet) in southern Norway, three putative Atlantic herring populations (Norwegian spring spawners = NSS, Coastal Skagerrak spring spawners = CSS, and local Landvik herring = LV) have previously been described to mix during the spawning season based on analyses of vertebral counts, otolith shape and somatic growth (Eggers et al., 2014) as well as behavioural differences (Eggers et al., 2015). However, the actual timing and location of spawning events seems to be population specific; LV herring has peak spawning in May inside the lake, whereas the two other populations tend to spawn outside the lake in February-April (Eggers et al., 2014; Eggers et al., 2015).

In the present study, it is hypothesized that these populations have grown up under different environmental conditions resulting in phenotypic differences, and that they have adapted to the spawning time and location tightly linked to the season and conditions experienced when they hatched themselves. This hypothesis was tested by applying otolith microstructure analysis to a series of year classes of these populations traced over several spawning seasons and to link the daily otolith growth to presumed ambient temperatures experienced by successive larval cohorts. Our hypothesis would allow for population discrimination which, in general, is extremely important not only from ecological point of view but also because of frequent difficulties in stock management. The ecological impact, in terms of losing biodiversity due to sub-optimal exploitation and consequently overfishing of populations, would be immense when population discrimination fails (Begg et al., 1999). Further, existence of population-related differences in otolith microstructure on a small-scale basis will be investigated.

2. Material and methods

2.1. Study area

The study area consists of Landvikvannet and the adjacent fjord (Strandfjorden) along the Norwegian Skagerrak coast (Fig. 1). Strandfjorden has fully marine conditions and is sheltered from the outer coast. The inner part, where samples were collected, is relatively deep (10–13 m) compared to the outer part which is narrow and shallow (1–7 m). Landvikvannet (1.85 km^2) is connected to Strandfjorden and further the open ocean by a 3 km long and narrow 1–4 m deep canal constructed in 1877. This construction allowed marine organisms to enter Landvikvannet from Strandfjorden. Landvikvannet has average depth of 10 m and a maximum depth of 25 m. The saltwater inflow from Strandfjorden and the freshwater from streams result in a highly stratified water column with a transition depth at 4 m. Typically, in May the upper layer has low salinity (< 20), high temperature (> 10 °C) and oxygen content above 5 ml/l. In contrast, the lower layer has high salinity, low and constant temperature (8 °C) and no oxygen (for details, see Eggers et al., 2014).

2.2. Biological data

Adult herring were sampled with gillnets during the spawning season (February-June) between 2012 and 2015 in Landvikvannet and Strandfjorden (Table 1). The maximum sample size was 100 herring per location and sampling date. According to previous results (Eggers et al., 2014) herring were separated into three different populations: Norwegian spring spawners (NSS, n = 139) were separated by subjective otolith shape based on a sharper distinction between winter and summer rings compared to local spring spawners. NSS were found in both Landvikvannet and Strandfjorden. Coastal Skagerrak spring spawners (CSS, outside the lake, n = 333), and Landvik herring (LV, inside the lake, n = 359) were separated by sampling location only (Fig. 1). In total, all 831 available otoliths of adult herring were extracted and analysed. For this study herring of four consecutive year classes, 2009–2012, were chosen (Table 2). Metric (e.g. length, weight) and meristic (number of vertebrae) characters, were measured for each individual herring. Otoliths were extracted for age reading and further analysis of daily otolith growth.

2.3. Environmental data

Ambient temperature is the main factor affecting larval growth (Folkvord et al., 2004; Fey, 2006; Oeberst et al., 2009), and in the present study ambient temperature both during the larval stage and at successive spawning events of the same year class were estimated. Environmental data were measured on the same day as the adult herring were sampled, both in Strandfjorden and in Landvikvannet (Fig. 1, Table 1). Data from the sampling date were averaged for all depths below 2 m in Strandfjorden and between 2 and 5 m in Landvikvannet. The depth was limited to 5 m in Landvikvannet due to anoxic conditions below this depth (Eggers et al., 2014). These values were used as proxies for the spawning temperature. Therefore, only spawning herring (maturity stage = 6, Mjanger et al., 2012) were used for the analyses including ambient water temperature at spawning (Table 1). The majority of non-spawning herring were close to spawning (stage 5). Therefore, the overall temperatures during spawning might be slightly higher, but should not influence the analysis. In addition, continuous temperature measurements from the IMR Flødevigen marine stations (approximately 20 km northwards) were used to calculate mean temperatures for the period when the measured daily otolith increments were generated. Temperatures were measured each day in 1 m and 19 m depths. In general, the seasonal temperature trends were the same in Strandfjorden, Landvikvannet and Flødevigen (Fig. S1). Hence, the data from Flødevigen was used as proxies for the estimation of temperatures during the larval stages.

2.4. Otolith analysis

Otoliths were fixed to glass slides with thermoplastic glue with the sulcus side up and ground with sandpaper (600 and 1200 grid) until the sulcus disappeared. The slides were reheated and the otoliths turned over carefully. Further grinding and polishing was conducted until the nuclei (core) were visible. To avoid over-polishing, the otoliths were repeatedly checked under a Leica DMLB light microscope (Leica Microsystems, Wetzlar, Germany; 40 x magnification) and digital images were taken with a Nikon DS-Fi2 digital camera. From the calibrated digital images (2560 × 1920 pixels) the daily increments were detected and measured using the Caliper function in Image Pro-Plus® version 7.0 (Media Cybernetics, USA). Each otolith annotation was individually verified after the automatic software detection and missing or additional increments were manually added or removed, respectively. Daily increments were registered from the core up to a distance of 170 µm from the core. Only increments with a minimum distance of 20 µm from the core were used for the analyses, because earlier developed increments are not necessarily daily or easily discernible (Geffen, 1982; Campana et al., 1987; Fox et al., 2003).

2.5. Statistical analysis

All statistical analyses and plotting were conducted in the R software (R Core Team, 2016). For all tests, we used the 95% level as the level of significance.

For statistical analyses, we used linear mixed-effects models to indicate the influence of different characteristics on the daily otolith growth of larval herring. The modelling followed a backward selection approach incorporating all fixed and random effects. First the optimal structure of the random effects was tested using likelihood ratio test based on the models fitted by restricted maximum likelihood estimations (REML) (Zuur et al., 2009). Also based on REML fits, the fixed effects structure was optimized using marginal *F*-statistics (Pinheiro and

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