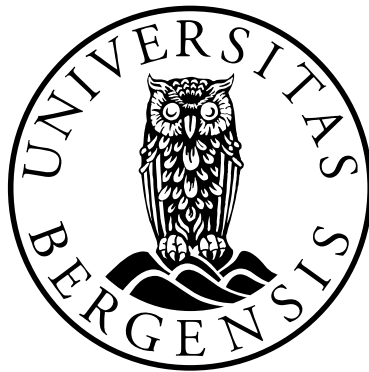


# **Metapopulation dynamics and behaviour of Atlantic herring (*Clupea harengus* L.) in a small semi-enclosed ecosystem**

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## Scientific environment

This thesis was conducted at the Institute of Biology (University of Bergen) and the Institute of Marine Research. The candidate, Lise Langård, has been affiliated with the research group *Fisheries ecology and Aquaculture* and *Pelagic Fish*. This work was funded by the University of Bergen and the Institute of Marine Research.





*It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is the most adaptable to change.*

Charles R. Darwin

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My first introduction into the world of herring was when I was given the opportunity to help out on a research cruise in Lindåspollene in 2006. There I had the privilege of working with a great team who sparked my interest in herring, and I have been a part of the “herring team” at the University of Bergen (UoB) and the Institute of Marine Research (IMR) ever since.

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Illustration: Åse Husebø

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## List of publications

This thesis is based on the following publications and manuscripts, and will be referred to in the text by their roman numerals (I-VI).

- Paper I:** Johannessen A, Nøttestad L, Fernö A, Langård L, Skaret G (2009) Mixing of stocks within the same school during spawning: support for a metapopulation in Atlantic herring? *ICES J Mar Sci* 66: 1740-1748
- Paper II:** Johannessen A, Langård L, Slotte A, Skaret G, Husebø Å, Fernö A. The dynamics of a metapopulation: changes in life history traits in local herring following increased connectivity with oceanic herring. *Manuscript Plos one*
- Paper III:** Langård L, Slotte A, Skaret G, Johannessen A. Thermal stratification influences maturation and timing of spawning in a local herring population. *Submitted manuscript J Fish Biol*
- Paper IV:** Langård L, Fatnes OA, Johannessen A, Skaret G, Axelsen BE, Nøttestad L, Slotte A, Jensen KH, Fernö A. State-dependent spatial dynamics in pre-spawning herring (*Clupea harengus* L.): site fidelity within a semi-enclosed coastal marine ecosystem. *Submitted manuscript Mar Ecol Prog Ser*
- Paper V:** Langård L, Johannessen A, Fernö A, Nøttestad L, Skaret G, Slotte A, Røttingen J, Øvredal JT (2012) Acoustic tagging: a suitable method for the study of natural herring behaviour around spawning? The Effects of Noise on Aquatic Life, *Adv Exp Med Biol* 730: 383-385
- Paper VI:** Langård L, Skaret G, Jensen KH, Johannessen A, Slotte A, Nøttestad L, Fernö A. Tracking individual herring within a semi-enclosed marine ecosystem: Meso-scale horizontal and vertical dynamics from pre- to post-spawning. *Manuscript Mar Ecol Prog Ser*



**Abstract**

Atlantic herring (*Clupea harengus* L.) is widely distributed throughout the North Atlantic Ocean. Detailed studies on its life history traits, migration behaviour as well as meristic and morphometric characteristics have revealed large variations in the spatial distribution of populations. As a result, Atlantic herring is often referred to as “population rich”, due to its complicated population structure. Along the Norwegian coast there appears to be a mixture of migrating oceanic herring, such as the Norwegian spring spawning (NSS) herring, and more stationary herring with the entire life cycle adapted to fjords and inshore areas. An overlap between these populations primarily occurs during the NSS herring’s overwintering and spawning periods, and as a result there is some uncertainty about the dynamics and level of interaction between the stationary and migratory herring populations during these periods.

This thesis focuses on Atlantic herring in Lindåspollene, a small semi-enclosed coastal marine ecosystem in south-western Norway. The thesis is based on fieldwork carried out during the spawning period using both passive and active acoustics in combination with biological and environmental sampling. The objectives were to explore the general spawning behaviour in herring by examining the small-scale processes of schooling dynamics down to the individual level and to explore whether the metapopulation concept could describe the herring dynamics taking place in this area.

The NSS herring stock collapse in the late 1960s resulted in a distributional and migratory shift, bringing the NSS herring closer to the Norwegian coast, increasing the spatial and temporal overlap with the more stationary coastal populations. By investigating different characteristics of the herring, such as growth patterns in combination with mean number of vertebrae (VS), different herring components could be distinguished. These components, interpreted as local and NSS herring, were found to occur together in the same school over several months with the degree of presence of the different components changing throughout the 50-year study period. The results show a clear overlap in spawning time between the components

supporting mixed spawning. The study further showed that an increased connectivity and genetic exchange over time changed several life history traits of the local herring, with regard to growth, age, size and length at first maturity. Despite these changes, along with the inflow of NSS herring, the local herring still aggregated in a single school and maintained the same position within the study area and remained there until spawning commenced in all years of study.

A series of field observations were made to study how maturation affects schooling of herring both on the school and individual level. This provides new information about individual priorities of spatial positioning both vertically and horizontally during a phase of potentially conflicting interests. State-dependent behaviour was observed on both levels throughout the spawning season and indicated that the components did not form distinct groups. A local adaptation was found with regard to timing of spawning, which deviated from the general assumption that maturation rates and spawning time in herring is tightly linked to the ambient temperatures during the maturation phase. Instead, the timing of spawning was found to be strongly related to thermal stratification in response to spring warming.

The findings from Lindåspollene offer new insight into the behavioural plasticity displayed by fish schools and it emphasises the transfer value of results obtained from small-scale studies to large-scale open ocean ecosystems. Our results strongly support that Atlantic herring form a metapopulation and for the first time demonstrates strong dynamics between the components over an extended period of time. This thesis also sheds new light on population structure of coastal herring populations with implications for the preservation of species- and population- diversity along the Norwegian coast and future management. Understanding the physical and biological factors that contribute to marine connectivity is critical to the implementation of marine conservation and management strategies, as these populations are vulnerable to overfishing. Unless precautions are taken, the number of differentiated fish stocks and the genetic variation within them are under threat of being reduced.

## Sammendrag

Atlantisk sild (*Clupea harengus* L.) kalles ofte “populasjonsrik” på grunn av sin komplekse populasjonsstruktur i forhold til livshistorietrekk, migrasjons-adferd, samt gyte-tidspunkt og lokalitet. Til tross for det omfattende arbeidet som er gjort på atlantisk sild, er det fortsatt diskutert hvordan sildepopulasjonene er strukturert i tid og rom. Langs norskekysten finnes det en blanding av vandrende oseanisk sild, norsk vårgytende (NVG) sild som oppholder seg langs kysten under overvintring og gytseasonen, og mer stasjonær sild som har tilpasset seg en hel livssyklus i fjorder og kystnære områder. Basert på denne blandingen er det stor usikkerhet om graden av overlapp i fordelingen mellom NVG sild og de stasjonære populasjonene.

Denne avhandlingen fokuserer på atlantisk sild i Lindåspollene under gyteperioden, i et lite semi-lukket marint økosystem i sørvest-Norge. Arbeidet er feltbasert, hvor det er brukt passiv og aktiv akustikk i kombinasjon med biologisk og miljømessig prøvetaking og observasjoner. Formålet med avhandlingen er å undersøke den generelle gyteatferden hos sild ved å konsentrere seg om småskala-prosesser av stim-dynamikk, både innad i stimen og ned til individ-nivå. Arbeidet beskriver også undersøkelser som vurderer om metapopulasjonskonseptet kan beskrive sildepopulasjonsdynamikken.

Kollapsen i NVG sildepopulasjonen på slutten av 1960-tallet førte til at NVG silden flyttet seg nærmere norskekysten som økte sannsynligheten for romlig og temporal overlap med de stasjonære populasjonene. Basert på ulike karaktertrekk, som for eksempel vekstmønster i kombinasjon med virveltall (VS) kunne ulike sildekomponenter identifiseres til lokal sild og NVG sild. Komponentene forekom sammen og graden av tilstedeværelse av de forskjellige komponentene endret seg over en 50-års periode. Det var en klar overlapp i gytetid mellom komponentene, som derfor støtter hypotesen om blandet gyting og at økt tilkobling og genetisk utveksling over tid har endret flere livshistorietrekk til den lokale silden, f.eks. innen vekst, alder, størrelse og lengde ved første modning. Til tross for disse endringene og insig

av NVG sild, fortsatte den lokal silden å samle seg hvert år i en stim på samme lokalitet til gyting startet.

Videre er en rekke feltobservasjoner beskrevet for å finne ut hvordan modningsgrad påvirker aggregering av sild både på stim og individ-nivå, som avdekker ny informasjon om dynamikken av silden under gyteperioden. Tilstandsavhengig adferd ble observert gjennom gytesesongen både på stim- og individnivå. En lokal tilpasning ble funnet i tilknytning til tidspunkt for gyting, hvor dette er et avvik fra den generelle antagelsen om at modningsgraden og tidspunktet for gyting hos sild er knyttet til temperatur i modningsfasen. Isteden var tidspunktet for gytingen sterkt relatert til lagdeling av vannmassene på grunn av oppvarming av overflatevannet.

Resultatene fra Lindåspollene gir ny og verdifull innsikt om graden av adferdsmessig fleksibilitet som vises av fisk i stim, og understreker overføringsverdien av resultater fra mindre studier til store økosystem i de åpne havområdene. Resultatene våre støtter at atlantisk sild utgjør en metapopulasjon og viser for første gang en sterk dynamikk mellom komponenter over en lengre tidsperiode. Avhandlingen kaster nytt lys over populasjonsstruktur av kystnære sildepopulasjoner, og dette vil ha positive innvirkninger for videre arbeid innen vern av arten og populasjonsmangfoldet langs norskekysten, samt framtidig forvaltning. Ved at disse populasjonene er sårbare ovenfor overfiske er forståelse av fysiske og biologiske faktorer som bidrar til marin tilkobling kritisk for å gjennomføre marint vern og forvaltningsstrategier. Forholdsregler må inngå som en del av forvaltningsprogrammer for å unngå en reduksjon av antall ulike fiskebestander og den genetiske variasjonen dem imellom.

## 1. Background

### 1.1 General basis for the thesis

Understanding the structuring of fish populations is essential in order to develop sustainable fisheries management (Wildes et al. 2011). There is a high degree of uncertainty as to the nature and extent of temporal and spatial population structuring among highly mobile, commercially exploited species (Smedbol et al. 2002, Kritzer & Sale 2004, Mariani et al. 2005, Wright et al. 2006, Bekkevold et al. 2011). Data on the extent of such structuring are vital to our capacity to manage and conserve declining stocks (Palumbi 2003), and fundamental when predicting responses to continued harvesting and environmental variability (e.g., Hauser et al. 2002, Turner et al. 2002, Hutchinson et al. 2003, Hoarau et al. 2005). Understanding how population dynamics of organisms play out in a dynamic, patchy habitat is critical to good conservation. Disregarding population differences in spatial distribution throughout their life cycle will influence the viability of populations, their capacity to recover from low levels of abundance and their evolutionary potential. To avoid overexploitation it is important to know whether individual fish harvested at any one location represent one or several populations (Jørgensen et al. 2005a).

The dynamics of the population structure in Atlantic herring have been widely discussed. Two opposing concepts have been put forward: Iles & Sinclair (1982, member/vagrant hypothesis) subdivide the herring into discrete population units, with separate life cycles and limited gene flow, whereas, the dynamic balance population concept (Smith & Jamieson 1986) considers the herring to consist of dynamic and relatively unstructured assemblages, implying that there are no barriers to exchange between spawning grounds or spawning populations. McQuinn (1997a) combined these concepts and argued that the herring population structure is more of a behavioural rather than genetic nature, which is referred to as the metapopulation concept (adopted-migrant hypothesis). A metapopulation is a set of local populations or subpopulations within a larger area (usually the population's range) where movement between populations is likely (Hanski & Simberloff 1997), with variable

but moderate interbreeding between subunits (Levins 1969, 1970), thereby describing the spatial dynamics of interconnected subpopulations. The metapopulation concept has been applied to explain population structuring of many species, ranging from the terrestrial (e.g., mountain sheep (*Ovis canadensis*; Bleich et al. 1990), Glanville fritillary butterfly (*Melitarea cinxia*; Hanski et al. 1995)), to marine fish (e.g., coral reef fish; Kritzer & Sale 2006, Saenz-Agudelo et al. 2012, plaice (*Pleuronectes platessa*); Hunter et al. 2003, walleye pollock (*Theragra chalcogramma*); Bailey et al. 1999, Atlantic herring (*Clupea harengus*); e.g., McQuinn 1997a, Atlantic cod (*Gadus morhua*); e.g., Robichaud & Rose 2001, Smedbol & Wroblewski 2002, Wright et al. 2006, Heath et al. 2008, Rose et al. 2011 and weakfish (*Cynoscion regalis*); Thorrold et al. 2001)), to the freshwater environment (estuarine and diadromous fish (Jones 2006) and salmon and other anadromous fish (Schtickzelle & Quinn 2007)), to invertebrates (Mumby & Dytham 2006) and giant kelp (Reed et al. 2006).

The metapopulation concept was primarily developed to model extinction-recolonization capacity within a network of habitat patches (Levins 1969, 1970). It has since been applied to local populations or subpopulations of organisms whose dynamics are strongly dependent on local demographic processes, such as fecundity, recruitment and mortality (Harrison & Taylor 1997, Hanski 1999, Kritzer & Sale 2004). The concept of metapopulations differs from that of the classic stock concept when applied to marine fish populations. The traditional way of viewing stock structure is static, whereas the spatial patterning of subpopulations is temporally dynamic within a marine metapopulation (e.g., extinction-recolonization). McQuinn (1997a) suggests that the gene flow between many herring stocks may be sufficient to define them as belonging to the same metapopulation. However, no clear evidence has yet been obtained for interbreeding of herring stocks (McQuinn & Lefebvre 1995, McQuinn 1997a, Smedbol & Wroblewski 2002). The metapopulation concept is increasingly being applied in marine science, although its applicability is still debated (Smedbol et al. 2002). This is often as a result of different definitions used among

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scientists resulting in misleading conclusions (Hanski & Simberloff 1997, Smedbol et al. 2002).

Distribution and aggregation patterns of pelagic fish in marine ecosystems are hard to predict and understand. Herring spend most of their life in schools (Blaxter & Hunter 1982, Fuiman 1989) and as herring go through different life history and seasonal phases, the schooling dynamics change resulting in highly dynamic and poorly understood schooling behaviour. Schooling dynamics and collective trade-offs are vital in order to improve our understanding of the spatio-temporal distribution and school patterns in pelagic fish species which has crucial implications for acoustic abundance estimation and stock assessment. Furthermore, if we aim at understanding schooling dynamics it is necessary to know how individuals behave and interact and why they apply such behaviours. It is therefore important to learn more about individual herring behaviour.

In order to provide an overview of the complex population dynamics and behaviour in herring in this thesis, I first define the different concepts used, and go on describing stock identification methods, general herring biology, information about Norwegian spring spawning (NSS) and local herring, the selected study area and the different scales used from the population level down to the individual level.

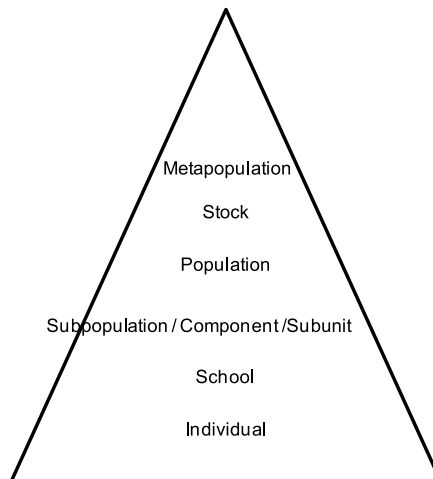
## **1.2 Definitions of concepts used in the thesis**

The terminology used in discussions of population structure and complexity is challenging, as there exists a wide range of temporal and spatial structures within population diversity. Terms used in this thesis are therefore defined as follows: *Connectivity* is referred to as the behavioural exchange of individuals among marine populations (Cowen & Sponaugle 2009), which does not necessarily involve genetic exchange. A *Metapopulation* as defined here is a special case of connectivity, which also involves exchange of genes. *Stock* is “an intraspecific group of randomly mating individuals with temporal or spatial integrity” (Ihssen et al. 1981). “A *Population* is a self-reproducing group of conspecific individuals that inhabit the same range at the

same time, are affected by similar environmental factors, and are reproductively isolated from other populations” (Smedbol & Stephenson 2001). “A *Subpopulation* is a semi-independent, self-reproducing group of individuals within a larger population that undergo some measurable but limited exchange of individuals with other areas within the population range” (Smedbol & Stephenson 2001). In this thesis, the term ‘*stock*’ is only used when it refers to fisheries assessment entities; otherwise the term ‘*population*’ is used. The terms *Subpopulation*, *Subunit* and *Component* are applied synonymously in this thesis, so component in **Papers I & II** is no different from subunit in **Papers II & VI** or subpopulation in **Paper V**. In this synopsis I will use the term component (Fig. 1).

Over the years, the term *School* has been subject to considerable debate and has resulted in several definitions (Wilson 1975, Partridge 1982, Pitcher 1983). ‘*School*’ has often been defined as fish swimming synchronously and polarised in groups, while ‘*shoals*’ includes all social groups of fish (including ‘*schools*’) (Pitcher 1983). However, there is still uncertainty in the literature, possibly as a result of past definitions of ‘*shoal*’ as a loose aggregation, or on account of the lacking distinction between ‘*school*’ and ‘*shoal*’ in many languages. In this thesis the term applied is ‘*school*’ and refers to a group of synchronously swimming fish. The term *culturally mediated behaviour* in this thesis is based on learned behaviour, not by genetics. In the same manner as traditions, which can be explained by learned behaviour that is passed on from one generation to the next (Wynne-Edwards 1962, Corten 2002), where subsequent generations may copy the behaviour and continue this specific behaviour for decades to come.





**Figure 1.** Overview of the different levels used in the synopsis in ascending order (metapopulation-individual).

### 1.3 Stock identification methods

The distinctness of populations within a metapopulation is usually evaluated by genetic analyses, primarily based on studies on allozymes, mitochondrial DNA (mtDNA) and microsatellites (e.g., Ryman et al, 1984, Dahle & Eriksen 1990, Shaw et al. 1999, André et al. 2011). Genetic studies can provide valuable insight in the population structure of herring (e.g., Bekkevold et al. 2007, Palsböll 2007), but seldom provide information about differences in relevant biological characteristics and there has been little concordance between meristic or morphological characters and genetic differentiation (Ryman et al. 1984, Clausen et al. 2007, Jørgensen et al. 2008). Recent genetic investigations in the North Sea herring using microsatellite DNA, allozyme and Single-Nucleotide Polymorphisms (SNPs) markers have found little differentiation among spatially discrete populations, but concordance divergence between populations in the Baltic and North Sea (Bekkevold et al. 2005, Larsson et al. 2007, 2010 Gaggiotti et al. 2009, Limborg et al. 2012). Teacher et al. (2013) further indicated that both temperature and salinity differences in the Baltic Sea may contribute to the patterns of genetic differentiation in Atlantic herring, and it has been shown that Atlantic cod (*Gadus morhua*) seem to have adapted to local temperature (Star et al. 2011) and salinity (Larsen et al. 2012) conditions. The frequently used

microsatellite DNA has a limited ability to fully resolve the population structure of species with comparatively high levels of gene flow (Waples 1998, Hutchings et al. 2007). Studies on population structure in the northeast Atlantic have normally suggested little divergence among the populations when using mtDNA (Dahle & Eriksen 1990). Furthermore, different genetic markers reflect different demographic histories as well as having varying statistical properties that influence the extent to which they can elucidate the divergence patterns (Awise 2004, Ryman et al. 2006, but see Knutsen et al. 2011).

Based on the information mentioned above genetic markers alone may not be powerful enough to distinguish between fish stocks (e.g., Nielsen et al. 2009, Svedäng et al. 2010). Therefore, non-genetic approaches may be required in order to understand connectivity with regard to the metapopulation concept (Svedäng et al. 2010). Svedäng et al. (2010) applied three independent methods in order to distinguish between cod stocks in Kattegat and the eastern North Sea and found that in spite of no genetic stock differentiation in cod, results from tagging and otolith studies identified discrete spawning grounds at close distances (<100 km). Population genetic studies have also demonstrated that the Norwegian coastal cod may be structured into local populations on small scales (Pogson & Fevolden 2003, Dahle et al. 2006, Westgaard & Fevolden 2007, Knutsen et al. 2011), down to the level of individual fjords (Jorde et al. 2007, Olsen et al. 2008).

In addition to genetics, different methods have been applied in order to distinguish between mixed herring stocks: 1) meristic (e.g., number of vertebrae (VS), gillrakers). VS is a phenotypic trait providing population information that reflects both environmental and genetic influences and is fixed relatively early in development, generally well before hatching and remains stable throughout life and may therefore represent the origin of the fish at spawning (Barlow 1961, Hempel & Blaxter 1961, Lindsey 1988, Hulme 1995, Pavlov & Shadrin 1998), 2) morphometric, (e.g., variation in dimensions of body parts and/or rates of change; e.g., Parsons 1975, Schweigert 1990), 3) parasitic load (variation in number and type of parasites), providing evidence of separate areas of origin of adults on feeding grounds (e.g.,

Chenoweth et al. 1986, Campbell et al. 2007), 4) trace element composition in calcified parts which can be used to infer stock structure and population connectivity (otolith microstructure; e.g., Brophy & Danilowicz 2002, Clausen et al. 2007, otolith morphometric analysis; e.g., Turan 2000, Burke et al. 2008), and 5) tagging, providing evidence of migration from one location to another (e.g., Harden-Jones 1968, Wheeler & Winters 1984a, b, Hay et al. 2001b). There are, however, limitations related to all these above-mentioned techniques, because the physical environment affects the expression of traits over the life of an individual, thus potentially merging non-heritable traits. This will have larger consequences for migratory species, which experience different environments over larger distances, thereby contributing to an increased variability in the non-heritable traits among populations, making population-specific differences difficult to interpret (McPherson et al. 2001). Genetic analyses have been conducted on historical microsatellite DNA from otoliths in Atlantic cod, which were stored dry in paper envelopes (Ruzzante et al. 2001), but in this thesis, genetic time series analyses could not be conducted as herring otoliths were prepared with histokit. Since herring show high phenotypic plasticity and strong responses of meristic characteristics in the environment, these environmentally regulated meristic or morphometric features are often more suitable when characterizing herring populations compared to the standard genetic techniques (McQuinn 1997a, McPherson et al. 2001, Brophy et al. 2006). However, advances in various techniques (microsatellites; Gaggiotti et al. 2009, Teacher et al. 2013, otolith microchemistry; Geffen et al. 2011, microstructure of the otolith core; Bierman et al. 2010, SNPs; Lamichhaney et al. 2012, Corander et al. 2013, microsatellites, allozymes, mtDNA; André et al. 2011) have led to improved population classification.

## **1.4 Herring biology**

### **1.4.1 Stock structure**

In spite of the long history of research on the general biology, ecology and genetics of Atlantic herring (*Clupea harengus* L.) (Blaxter & Hunter 1982, Whitehead 1985,

Mariani et al. 2005), there is still no general agreement as to how herring populations are spatially and temporally structured (Mariani et al. 2005, Reiss et al. 2009). Atlantic herring are found across the northern Atlantic, inhabiting the Eastern Atlantic, the Baltic Sea, and the Western Atlantic and spawn in coastal areas, but their distribution during feeding may be oceanic or confined to more limited local areas (Hay et al. 2001a). It is a complex species and herring stocks represent a wide range of life history strategies, spawning seasons and locations (Jennings & Beverton 1991, McQuinn 1997a), as well as genetic structuring (e.g., Bekkevold et al. 2005, André et al. 2011). The Atlantic herring is geographically isolated and genetically distinguishable from the Pacific herring (*Clupea pallasii*; Grant 1986, Domoanico et al. 1996), and has to a large extent been separated based on geographical barriers between spawning locations or phenotypic differences (Heincke 1898, Hulme 1995, Jørgensen et al. 2005b, 2008, Bekkevold et al. 2007). Genetic stratification is likely determined by mechanisms of natal homing, larval retention and natural selection (Bekkevold et al. 2005, White et al. 2010).

Each year herring may undertake long distance feeding and overwintering migrations (Stabo 1982, 1987, Moulund et al. 2003, Waters & Clark 2005) where the different stock components mix (e.g., Husebø et al. 2005, Ruzzante et al. 2006, Bekkevold et al. 2011), but they separate during the spawning season (Wheeler & Winters 1984a, Messieh et al. 1989, Rosenberg & Palmén 1981, Stephenson & Kornfield 1990, Burke et al. 2008). In the northeast Atlantic, the herring populations are generally divided into two categories: coastal/fjord stocks and oceanic stocks (such as NSS and North Sea herring) (Holst et al. 2004, Husebø et al. 2005). Herring utilises homing as they annually return to spawning grounds and show fidelity to the spawning area from which they have originated (e.g., Messieh & Tibbo 1971, Hourston 1982, Iles 1986, Wheeler & Winters 1984a, b, McQuinn 1997a). As a result this has led to a general agreement that the herring maintain population integrity and persistence by repeatedly returning to spawn at specific spawning grounds (McQuinn 1997a).

Population complexity occurs on both sides of the Atlantic and Pacific (Hay et al. 2001a). This thesis investigates in detail population mixing over a specific time

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period at the Norwegian coast. A main part of this study is based on the hypothesis that metapopulation dynamics is taking place among herring along the Norwegian coast where there appears to be a mixture of oceanic herring visiting the coast during the overwintering and spawning seasons, and more stationary herring adapted to life cycles in fjords and inshore areas. The main type of oceanic herring visiting the Norwegian coast is the NSS herring. The NSS herring has been found to differ both genetically and phenotypically from some of the local fjord populations in Norway (Jørstad & Pedersen 1986, Johannessen & Jørgensen 1991). The NSS herring also differs phenotypically (Ryman et al. 1984, Johannessen & Jørgensen 1991) from populations in the North Sea, Skagerrak, Kattegat and the Baltic Sea, whereas there seems to be small genetic differences between these stocks (Jørstad et al. 1991, Husebø et al. 2005, Jørgensen et al. 2005b, Larsson et al. 2007, 2010, André et al. 2011, Limborg et al. 2012, but see Corander et al. 2013, Teacher et al. 2013).

#### **1.4.2 Reproductive biology**

Herring lay demersal eggs and spawn in a broad range of environments from the deeper part of the continental shelf to the intertidal zone, as well as in a wide range of salinities and temperatures between latitudes 35°N and 70°N (Blaxter 1985). Within a population the environmental preferences that favour the survival of eggs and larvae may be specific, resulting in spawning at distinct times and locations (Haegele & Schweigert 1985). Consequently, the maturation rate or spawning time varies with observed temperatures in herring and is indicated to be an adaptation to match emerging larvae to available food in spring plankton blooms (Hay 1985, Ware & Tanasichuck 1989). This is in agreement with the match-mismatch hypothesis, which takes into account the timing, as related to the phytoplankton blooms triggering the emerging zooplankton as food for herring larvae (Cushing 1990). The maturation process could also be synchronised by pheromones (Scott et al. 1994). The maturity stages of individual fish differ amongst and within the schools or populations at the same site during spawning (Nøttestad et al. 1996, Axelsen et al. 2000), and morphological and structural features of herring schools change markedly over time,

resulting in a highly dynamic and poorly understood schooling behaviour (Nøttestad et al. 1996, Axelsen et al. 2000, Skaret et al. 2003).

Herring spawn demersally up to 10-15 times during a lifetime (Blaxter & Hunter 1982, Slotte 1999a) and over a relatively short period annually (Blaxter & Hunter 1982), where eggs are attached to the bottom substratum (Hay et al. 2001a). Eggs are all released within a single spawning period, with the number of eggs increasing with female size. The preferences for both spawning substrate and depth vary from population to population (Runnström 1941b, Blaxter & Hunter 1982, Haegele & Schweigert 1985). Both Atlantic (Lambert 1987, Lambert & Messieh 1989) and Pacific (Hay 1985, Ware & Tanasichuck 1989) herring have been observed to spawn in up to 4 waves. The larger fish are the first to spawn and the first to leave the spawning grounds, while recruit spawners are the last to spawn (Lea 1929b, Harden Jones 1968). Individual herring may complete spawn deposition in a matter of hours (Pacific herring; Holliday 1958, Stacey & Hourston 1982). The duration of the spawning period may further be affected by school size (Stacey & Hourston 1982). Past studies have suggested that herring depend on light to spawn (Blaxter & Hunter 1982), but herring have been reported to spawn during dark hours (Furevik 1976, Kjørsvik et al. 1990, Johannessen et al. 1995). Herring larvae hatch after 2-4 weeks depending on temperature and the larvae drift along with the currents until metamorphosis (Dragesund et al. 1980, Corten 1986).

### **1.4.3 Life history traits**

Life history traits include characteristics such as growth, survival, age-at-maturation, fecundity, distribution and abundance (Ihssen et al. 1981, Pawson & Jennings 1996, Begg et al. 1999). Naturally occurring populations differ in life history, behavioural and morphological traits depending on their locality of origin (Pauli 2012). Within the same species, different components often occupy a wide range of different habitats and some parameters may change, reflecting the expression of different life history tactics. Intraspecific variation in life history traits (i.e., plasticity) has been demonstrated in numerous fish species, e.g., American shad (*Alosa sapidissima*;

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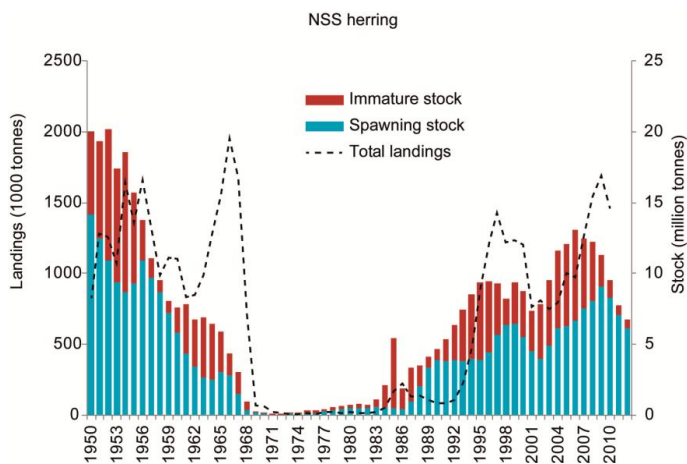
Leggett & Carscadden 1978), Atlantic herring (*Clupea harengus*; Jennings & Beverton 1991), European plaice (*Pleuronectes platessa*; Nash et al. 2000) and Atlantic cod (*Gadus morhua*; Thoresen et al. 2010).

Life history characteristics such as length at age and length at maturity may differ considerably between herring populations (Hay et al. 2001a). Changes in biological parameters such as growth (Casini et al. 2010), condition (Engelhard & Heino 2006) and spawning time (Óskarsson & Taggart 2009) are often explained as a result of climate change, but may also be affected by fluctuations in population structure and density (Engelhard & Heino 2004a, Casini et al. 2006, Óskarsson & Taggart 2009). Similar changes are also consistent in other fish species, such as capelin (*Mallotus villosus*; Carscadden et al. 1997, Orlova et al. 2010), sprat (*Sprattus sprattus*; Möllmann et al. 2005, Casini et al. 2006), North Sea cod (*Gadus morhua* L.; Chen et al. 2005) and northeast Arctic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus*) (Dingsør et al. 2007). Local variation in total length and maturity at age has also been demonstrated between cod from different fjords and coastal waters of northern Norway (Berg & Albert 2003), as well as along the Skagerrak coast (Olsen et al. 2004). As the environmental conditions experienced by a population change, adjustments in the age-specific patterns of growth, fecundity and mortality can occur as a result of phenotypic plasticity or by genetic selection (Wootton 1998).

## **1.5 Norwegian spring spawning (NSS) herring**

The NSS herring is known as the largest of all herring stocks, covering large parts of the northeast Atlantic, conducting extensive seasonal migrations between overwintering, spawning and feeding areas (Østvedt 1965, Devold 1968, Dragesund et al. 1980, 1997). For assessment and management purposes NSS herring is treated as a single stock (Husebø et al. 2005). The herring migration is closely related to its stock size and the stock abundance has undergone marked fluctuations in the last 60 years (Dragesund et al. 1997, Holst et al. 2002), which has resulted in changes of migration patterns, e.g., from oceanic to coastal and back to oceanic (Hamre 1990, Anon 1994). The stock declined throughout the 1950s and 1960s and collapsed close

to commercial extinction in the late 1960s (Fig. 2). Prior to the collapse, NSS herring had overwintering and feeding grounds in the Norwegian Sea and spawning occurred off the Norwegian coast from Møre (63°N) and southwards (Dragesund et al. 1980), and the spawning stock remained at extremely low levels throughout the 1970s and early 1980s (Hamre 1990, Anon 1994, Holst & Slotte 1998, Engelhard & Heino 2004a, b). The collapse was a result of high fishing pressure and low recruitment (Dragesund et al. 1980, Fiksen & Slotte 2002) and it took over 30 years to rebuild the stock (Holst et al. 2002).



**Figure 2.** Stock size and landings of NSS herring from 1950 to 2012 (Institute of Marine Research 2013).

NSS herring spawn demersally on stony or rocky bottom at depths down to 250 m (Runnström 1941b, Dragesund 1970a). At the population level, the duration of the spawning period in NSS herring is about four weeks (Devold 1967, Johannessen et al. 1995), with a midpoint in the first weeks of March (Toresen 1991), while spawning at the school level has been found to be completed within a few days (Aneer et al. 1983, Kjorsvik et al. 1990, Nøttestad et al. 1996, Axelsen et al. 2000, Skaret et al. 2003). Depending on where the larvae hatch, they will either drift northwards along with the coastal current to nursery areas in fjords and in the Barents Sea (Dragesund et al. 1970a, Slotte 1998, Vikebø et al. 2010), or be carried out to sea (Wiborg 1957, Johannessen et al. 1995). The adolescent NSS herring leave the nursery areas and



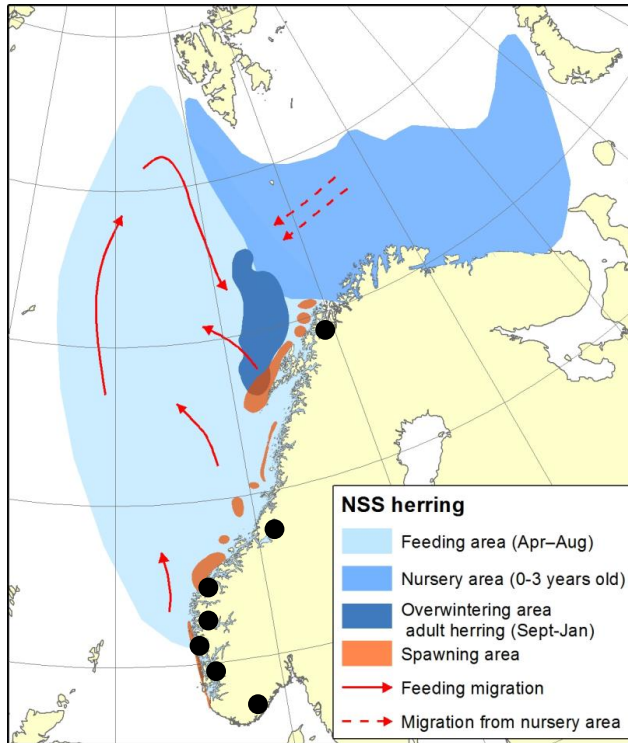
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enter the Norwegian Sea 1-2 years prior to first spawning, normally at age 2-4 years (Lea 1929a, b, Runnström 1936, Dragesund 1970a, b, Dragesund et al. 1980). The spawning migration starts in January and in the following months occurs on the banks along the Norwegian coast ranging from Lofoten to Lista (approximately 1500 km between 58°N and 70°). The utilisation of the spawning grounds (58° to 70°N, Runnström 1941a, b, Johannessen et al. 1995, Slotte & Dommasnes 1998) has varied markedly over the past 100 years (Dragesund et al. 1997). After spawning, feeding takes place in April to August involving extensive migrations in the Norwegian Sea, whereas winter months (September to January) are spent in large schools aggregating in deep areas (like fjords in northern Norway) where feeding ceases and movement is restricted to a minimum (Huse & Ona 1996, Slotte 1999b).

Juveniles of abundant year classes are in general associated with the Barents Sea, while the young of less abundant year classes are generally distributed in the coastal areas. As a rule the growth rate decreases northwards due to a large temperature range and ecological regimes, and accordingly herring originating from the coastal nurseries grow faster and mature at a younger age than the herring growing up in the colder Barents Sea (Holst & Slotte 1998, Husebø et al. 2007). It is probable that an oceanic population such as the NSS herring may go through changes in biological characteristics that are related to large-scale changes in the open ocean (Stige et al. 2006, Lehodey et al. 2006, Ottersen et al. 2010). The stock has a very dynamic recruitment pattern (i.e., variations in year class strength), providing natural variability in both the stock size and distribution patterns (Holst et al. 2004). NSS herring is highly migratory, covering large parts of the Norwegian Sea when the stock levels are high (Devold 1963, Dragesund et al. 1980, Hamre 1990, Holst et al. 2002) and is characterized by a high stable length at maturity, but a variable age depending on density (Engelhard & Heino 2004a, b) and has developed a suite of reproductive strategies (Óskarsson et al. 2002, Kennedy et al. 2010, 2011). The spawning migration distance seems to increase with the length and condition of the fish (Slotte 1999a, b, Slotte & Fiksen 2000, Slotte et al. 2000). According to the stock size, different proportions of the stock will spawn in different areas as a result of density-dependence (Holst et al. 2004).

## 1.6 Local herring

Along the Norwegian coast there are a number of small fjords and semi-enclosed bays and polls, where small, more or less self-contained herring populations exist (Lie et al. 1978). These fjord or coastal stocks typically have a small stock size and a limited distribution compared to the large stock sizes of the oceanic stocks like the North Sea and NSS herring, that are broadly distributed and perform long-distance migrations (Holst et al. 2004, Husebø et al. 2005). The local populations may adapt its maturation of spawning to the local conditions. The local stocks appear to have evolved different life history traits than the highly migrating oceanic components of NSS herring (mean vertebral count, VS >57) and are generally characterized by slower growth, low VS (55-56) shorter life span and higher relative fecundity (Hognestad 1994, Jørstad & Nævdal 1981, Sørensen 2012, Silva et al. 2013). Compared to an oceanic population, a small fjord population may be more affected by changes in the local conditions and the inflow of NSS herring. The biology and population dynamics of the local herring populations have not been extensively investigated, however, a few stocks have been studied along the Norwegian coast (Aasen 1952, Broch 1908, Rasmussen 1941, Lie et al. 1978, Jørstad & Pedersen 1986, Fig. 3). The geographical distribution, migration pattern, meristic and morphological traits are essential factors in the separation of these stocks.



**Figure 3.** Overview of the NSS herring distribution throughout the year. Filled circles represent known local herring populations (adapted from Havforskningsrapporten 2013, Fiske & Havet 1).

### 1.7 Connectivity between NSS and local herring

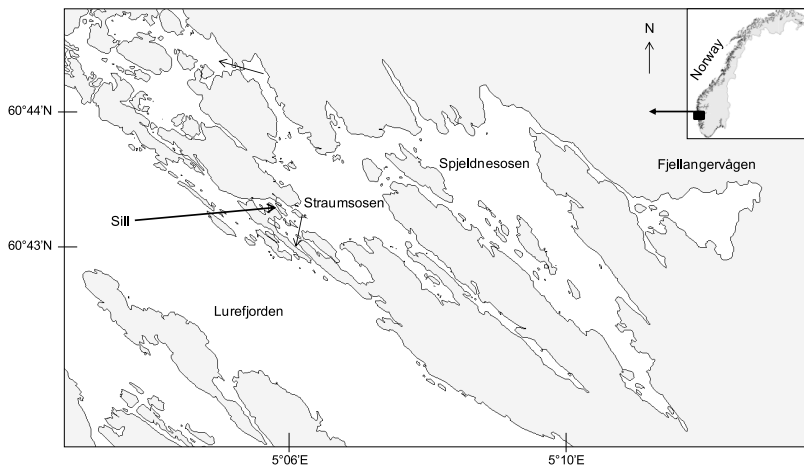
After the stock collapse, the remaining NSS herring grew up along the coast and remained in coastal waters to overwinter, spawn and feed more inshore than before the collapse (Dragesund et al. 1997, 2008, Røttingen 1992). This situation lasted throughout the 1970s until the rich 1983 year class growing up in the Barents Sea restored the former oceanic migration pattern (Dragesund et al. 2008). During the rebuilding period, the majority of the progeny grew up in coastal nursery areas instead of the Barents Sea with the distribution of juvenile herring in coastal and inshore waters more restricted than earlier (Dragesund 1995, Holst & Slotte 1998, Holst et al. 2002, Dragesund et al. 2008). Year classes originated almost entirely from local coastal regions, with marginal contributions from the Barents Sea (Holst &

Slotte 1998). This distributional shift brought NSS herring closer to the local populations along the coast (Holst & Slotte 1998) resulting in a high probability of mixing. Spawning takes place closer to the coast when the NSS herring stock levels are low resulting in a larger proportion growing up in the fjords (Dragesund et al. 1997, Holst & Slotte 1998). Past studies suggest that 0-group NSS herring generally utilize fjords as an overwintering area in the first year of life, and that by the next summer they migrate out of the fjord to feed (Devold 1963, Dragesund 1970b, Røttingen 1990). However, it has been suggested that some fish remain and undertake the first spawning under the same conditions as local herring before leaving the fjord/coast (Slotte 1993). Some remain close to the coast, with highly dynamic migrations and may even migrate back to the fjords after summer feeding for a second and third overwintering, before becoming oceanic mixing with the adults. Yet, little information exists on how stationary the local populations are, and whether they actually interbreed with migrating populations.

## **1.8 Characteristics of the study area**

A prerequisite for the metapopulation concept is the regular interbreeding between populations as mentioned above, which is a major challenge to prove (McQuinn 1997a). When studying herring dynamics it is therefore of great advantage to be able to perform well-defined and controlled experiments at relevant scales within their natural environment and ecosystem (Nøttestad et al. 2004). This is, to a large extent, possible within the study area of the present thesis. Lindåspollene in south-western Norway is a small well-defined ecosystem covering about 7 km<sup>2</sup>, providing a simple system with favourable weather- and current conditions. It is a semi-enclosed coastal marine ecosystem connected with the outer sea via a main sill (Fig. 4), consisting of three distinct, 60 to 90 m deep basins. The relatively sheltered Lindåspollene differs from the outside with regard to environmental conditions, species abundance, and food organisms. It is characterized by moderate boat traffic, and only small-scale gillnet and hand line fishing is permitted, making it ideal for small-scale ecosystem studies (Dahl et al. 1973, Lie et al. 1978). A small local herring stock has been

regularly documented here since 1962 (Anon 1969), and is regarded distinct from NSS herring because of its deviating growth pattern and smaller size-at-age (Lie et al. 1978). Most of the herring lifecycle seems to be within this system, providing an opportunity to conduct studies on aspects of the life history and population dynamics of the herring, as well as studying behaviour both at the collective and individual scale. Lindåspollene is a self-contained fjord system but is influenced by the coastal ecosystem through migrations of herring, in addition to prey and predators. It is still unclear as to why the herring remain there decade after decade, but it could be connected to low predation pressure, sufficient food availability and predictable spawning conditions.



**Figure 4.** Map of the Lindåspollene system, comprising three basins; Straumsosen, Spjeldnesosen and Fjellangervågen. Lindåspollene is connected to the outer fjord system (Lurefjorden) through a main sill along with other inlets/outlets from Straumsosen (marked with arrows).

## 1.9 System levels of the study

In this thesis, Lindåspollene provides a natural model system in order to study the interactions and relationships between the different herring components mixing there. It additionally allows us to track changes over time and reveal new aspects of the dynamics occurring at different scales, from individual behaviour to ecosystem dynamics which can be monitored on a fine-scale with sophisticated technology

testing hypotheses. The focus in this thesis will be on three different scales; the population, collective and individual scale. These scales are described below.

### **1.9.1 The population scale**

Most studies examine population structure over relatively limited time periods (normally 2-3 years) (e.g., Kornfield et al. 1982, Grant & Utter 1984, King et al. 1987, McPherson et al. 2001). These “snapshots” provide biologically meaningful information about a species, in particular detailed studies between and within years, but they do not provide information about the temporal stability of discrete populations. In comparison, as the effect of metapopulation dynamics and interbreeding may take time. Long-term time series may provide crucial information regarding both temporal and spatial dynamics, and make it possible to track changes over time in life history, morphological or behavioural traits (such as growth, length at maturity, longevity, VS and spawning time), and thereby provide new opportunities to explore long-term changes in populations. Population studies in more enclosed systems, such as fjords or semi-enclosed systems are less expensive and may provide adequate opportunities to study the population dynamics, compared to studies in large areas. Furthermore, our studies were conducted in a small area, providing consistent comparisons over time and space. The herring inside Lindåspollene has been sampled since the 1960s, providing a spatial “snapshot” during the spawning period. The available biological data should provide a good basis for studies of changes within the population.

### **1.9.2 The collective scale**

In smaller local herring populations the dynamics are different compared to the larger oceanic herring, with shorter distances between pre-spawning and spawning areas and fewer individuals to join for protection (Fernö et al. 1998). How this affects the schooling dynamics is still unknown as well as how the influence of other herring components will affect the schooling behaviour. Studies of vertical and horizontal movements over the pre-spawning and spawning period at the collective scale could potentially reveal whether there are diverging or synchronous behaviour linked to

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changes in population structure and maturation as observed with biological sampling and whether different components spawn together. Schooling dynamics and collective trade-offs is paramount to improve our understanding of the spatio-temporal distribution and school patterns in pelagic fish species. Herring has been widely studied over a large range of different scales, particularly from large-scale in the open ocean studying annual migration patterns to meso-scale studies on spawning grounds of the school dynamics of herring and its predators (Nøttestad et al. 1996, Fernö et al. 1998, Axelsen et al. 2000, Slotte & Fiksen 2000, Slotte 2001, Skaret et al. 2003). Monitoring fish stocks using acoustics is highly influenced by how the fish aggregate and the dynamics of these aggregations (e.g., Frøen & Misund 1999). Generally, schooling fish are considered as making behavioural decisions to stay, join or leave a school occurring on a second-to-second time scale (Pitcher & Parrish 1993). Schooling behaviour also seems to be influenced by a number of abiotic factors, such as light level, weather conditions, water depth, temperature and oxygen (Glass et al. 1986, Scalabrin & Masse 1993, Weetman et al. 1999, Domenici et al. 2002, 2007). Schooling dynamics change as herring go through different life history and seasonal phases. The situation for herring changes considerably prior to, during and after spawning (Nøttestad et al. 1996) and the maturity stages of individual fish vary amongst and within the schools or populations at the same site during spawning (Axelsen et al. 2000), resulting in highly dynamic and poorly understood schooling behaviour (Nøttestad et al. 1996, Skaret et al. 2003). In other words, one has to be in the right place at the right time. In Lindåspollene the location of the local herring population is known, and therefore permit studies on schooling dynamics. Since herring has been observed acoustically (e.g., echosounder) inside the system since the 1960s, there is also a basis to evaluate whether there have been significant changes in the collective behaviour.

### **1.9.3 The individual scale**

Individual organisms are the basic building blocks and if we aim at understanding schooling dynamics we need to know how individuals behave and interact and why they apply such behaviours. Several studies have investigated behaviour on the

school level right before and during spawning (Nøttestad et al. 1996, Mackinson 1999, Axelsen et al. 2000, Skaret et al. 2003), but detailed studies of movement patterns of individual herring during the spawning period have not been conducted due to difficulties of long-term tracking. A prerequisite for such investigations is that schools are available for observations over extended periods of time. Tracking individual fish over long time periods may provide information about what kind of behavioural decisions individual fish make during critical processes, such as reproduction, which takes place on a short time scale and limited spatial scale, thereby presenting the opportunity to examine how individuals behave at different stages of the spawning process from pre-spawning until recovery post-spawning.

In the past, several techniques have been used to study herring migrations, including active and passive techniques such as mark-recapture (Fridriksson & Aasen 1950, 1952, Fridriksson 1955, Jakobsson 1963a, 1965, Anon 1964) and hydro-acoustics (Nøttestad et al. 1996, Axelsen et al. 2000, Skaret et al. 2003). Due to advances in technological developments, both with respect to types of tags and the range of data that can potentially be collected, it is now possible to acquire detailed information about life cycle properties of individual fish (Arnold et al. 2002). Acoustic tagging is an effective technique for locating individual fish with high accuracy (e.g., Meager et al. 2009, 2010, Skilbrei et al. 2009, 2010, Skjæraasen et al. 2011, Eggers 2013), providing continuous observations of individuals in their natural environment (Løkkeborg et al. 2002). In Lindåspollene, the conditions for tracking herring with an acoustic system are nearly ideal, given the limited distributional area.



## 2. Objectives

Based on the background information above the two main objectives were set up for the thesis: 1) to explore the general spawning behaviour in herring by examining the small-scale processes of schooling dynamics and behaviour within herring schools, and 2) to explore whether the metapopulation concept could describe the herring dynamics taking place in Lindåspollene on three different scales (Fig. 5).

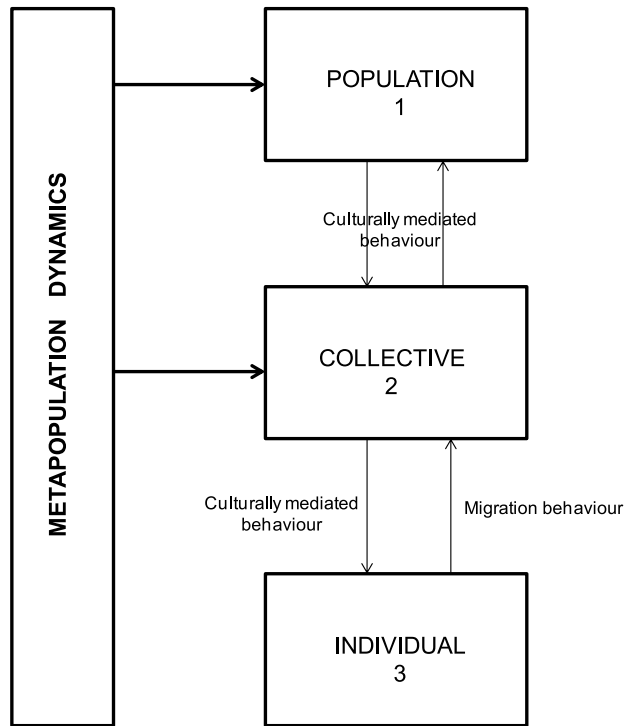
**Scale 1:** The population level: Analysis of biological data collected during 1962-2011, to explore whether metapopulation dynamics has occurred in the system; i.e., analyse whether there is an overlap in time, space and maturation of different herring populations, and whether this has caused any changes in life history traits. Including data on:

- Population structure (**Papers I, II**)
  - Vertebral count (**Papers I, II**)
  - Growth (**Papers I, II**)
  - Age and length at first maturity (**Paper II**)
- Timing of spawning (**Paper III**)

**Scale 2:** The collective level (**Paper IV**): Analyses of school parameters in the pre-spawning period over six consecutive seasons in order to study schooling dynamics in relation to the development and diversity in maturity state and adaptations to local conditions, providing insight into the dynamics of school behaviour. Explore whether the collective behaviour and cultural migratory pattern of the herring has remained the same since the 1960s or whether it is influenced by metapopulations dynamics by examining the schooling dynamics and behaviour.

**Scale 3:** The individual level (**Papers V, VI**): Analyses of individual swimming behaviour, vertical and horizontal distribution during the spawning season to explore whether herring would have diverging behaviour during and after spawning, whether

they are forming different groups in the area and having migrations comparable to that observed in earlier periods.



**Figure 5.** Conceptual framework of metapopulation dynamics at three different scales. The top-down effect represents how the population scale affects the collective and individual scale, and will depend on the inflow of NSS herring. The behavioural output is the result of how the metapopulation dynamics influences the different scales over time which is represented by the bottom-up effect on the different scales, e.g. with regard to migratory behaviour on the individual scale, and culturally mediated behaviour on the collective scale.

### **3. Summary of papers**

#### **Paper I:**

Several populations of Atlantic herring have been hypothesised to form a metapopulation with occasional genetic exchange between different components. A prerequisite for this hypothesis to be true is at least sporadic spatial overlap of individuals from different populations during spawning. This has previously not been demonstrated. We investigate a local population of Atlantic herring that has existed for several decades (possibly centuries) in the semi-enclosed coastal marine ecosystem of Lindåspollene in south-western Norway. During 2005-2007, potential spatio-temporal mixing of this local population with other herring populations was investigated prior to and during spawning. Acoustic recordings and biological samples from gillnet catches throughout the spawning period showed that local and NSS herring primarily mixed within one single main school. The results showed that NSS herring were significantly younger than local herring, but of about the same size with very similar gonad maturation pattern. Spent fish from both populations were also observed together in the gillnet samples. With increasing distance from the main school, NSS herring became more frequent compared to local herring. Our findings indicate interbreeding between the two populations, thereby supporting the hypothesis that several populations of herring in the northeast Atlantic make up a metapopulation. This study sets the basis for the thesis, opening up for possible hypotheses to be tested, but provides only a snapshot of what has taken place after the recovery of NSS herring.

#### **Paper II:**

Herring population dynamics is very complex and not fully explored. During the past 50 years, NSS herring have displayed marked changes in overwintering, spawning and feeding grounds, connected with the collapse in the late 1960s and its recovery in the 1980s. During this 50-year period the migration pattern changed from oceanic to coastal and back to oceanic. A local population of Atlantic herring was sampled by gillnets in the period 1962-2011 in south-western Norway. During this period several

components of herring identified by different growth patterns and vertebrae number occurred together in a semi-enclosed coastal marine ecosystem, with one component characterized by slow growth and low VS in the 1960s and another component with rapid growth and high VS only present until age 4-5. The situation varied throughout the 50-year time period with different components dominating in different decades, with marked changes from 1950-70 to the 1990-2000s. There was an overlap in spawning time between the components supporting mixed spawning. An increased connectivity and genetic exchange over time changed several life history traits of local herring with an increased age, growth rate and length at first maturity. The relative importance of genetic and cultural factors behind the changes in life history traits is discussed. Similar methods were applied as in **Paper I**, but this study provides a long time series of data from before the collapse until after the recovery.

### **Paper III:**

Maturation and timing of spawning in relation to temperature was studied in a local Atlantic herring population at the west coast of Norway. Lindåspollene is a relatively shallow 7 km<sup>2</sup> landlocked fjord, separated from the larger and deeper outer fjord area by sills with a depth of 3-10 m. In the present study a combination of CTD casts and biological sampling of gillnet catches in 2006-2010 demonstrated that very variable ambient temperatures experienced by the herring during the early pre-spawning (2-6°C) and late spawning phase (4-8°C) did not have significant effects on the timing of spawning. Instead, spawning was found to be triggered by the timing of thermal stratification as an effect of rapid spring warming that took place at about the same time every year regardless of initial temperatures. This study represents an example of a local population that has adapted to the environmental conditions, which may differ between herring living in oceanic, coastal and inshore areas.

### **Paper IV:**

Schooling dynamics and state-dependant trade-offs are paramount for our understanding of the spatio-temporal distribution and school dynamics in pelagic fish. We studied schooling dynamics of pre-spawning herring by means of *in situ* acoustic

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monitoring, such as an echosounder and sonar, and biological sampling. The primary objectives were to explore the hypothesis that local herring consistently aggregate in a single large school prior to spawning and to map the school dynamic features in relation to the progression and diversity in gonad maturity. In all years pre-spawning herring aggregated within a small area characterized by a trench leading to the deepest basin in the system. During the late pre-spawning period, the herring school was observed closer towards the spawning grounds. The school behaviour was state-dependent with the school more densely packed and more vertically compacted during late than early pre-spawning. A higher diversity in maturity stages between individual herring was assumed to be associated with a stronger inter-individual motivational conflict. Altogether, the results show that both the geographical positioning and the schooling dynamics of herring are state-dependent, which needs to be taken into consideration in herring behavioural studies. Our findings on schooling dynamics and the underlying ecological factors reflect general features of herring behaviour and should be relevant also for more coastal and oceanic populations. In order to understand the relationship between the individual and school level, it is essential to learn more about the individual herring behaviour (**Papers V, VI**).

#### **Paper V:**

As school dynamics are the output of behavioural decisions in individuals, it is essential to learn more about the behaviour of single fish. Herring schools can be studied by traditional acoustic methods (e.g., echosounder and sonar), but to understand the relationship between the individual and school levels as well as the interactions between components of herring, it is vital to learn more about individual herring behaviour. Acoustic tagging has successfully been used to track individual fish of various species, but herring are particularly difficult to tag due to scale loss during handling. Altogether 45 herring were tagged with internal acoustic transmitters in order to track pre-spawning and spawning individuals. The conditions for a tagging experiment in 2009-2010 were ideal as the herring remained in a single school for more than one month within an area of  $\sim 200 \text{ m}^2$  in a sheltered semi-

enclosed ecosystem. The study demonstrated that acoustic tagging is a suitable method to study natural behaviour in herring around spawning and provided the basis for **Paper VI**.

**Paper VI:**

Small-scale individual movement patterns of herring (*Clupea harengus* L.) inside a 7 km<sup>2</sup> landlocked fjord were studied during the spawning season using acoustic tags and a network of ultrasonic receivers. A total of 28 herring were tagged and tracked for up to 60 days. Altogether 24 fish remained within the poll throughout the spawning period showing fidelity towards a specific area during the pre-spawning period, gradually moving closer to the spawning grounds as maturation progressed and stayed in the outer basin closer to the coast after spawning. However, individual differences indicated individual strategies within the main pattern. Herring conducted marked diel vertical migrations (DVMs) before spawning, staying deeper during daytime, but the DVMs gradually decreased towards spawning, and when approaching spawning herring stayed close to the surface both during day and night. The results indicate that within a relatively short time span there is a development from a situation with predictable spatial positioning and strong group coherence, to a situation with high individual variability in spatial positioning reflecting variable states and behavioural decisions.

## 4. Discussion

This thesis demonstrates mixing of different components of Atlantic herring during the spawning period in a semi-enclosed ecosystem and provides evidence of metapopulation dynamics (**Papers I, II**) related to the large-scale variations in NSS herring abundance and migration pattern. A distributional shift associated with the collapse brought the NSS herring closer to the local populations along the Norwegian coast, which could increase the probability of mixing and interbreeding with the local population. Despite the occurrence of several components in the system and changes in several population traits, herring in all years aggregated in a single school at the same location until spawning commenced suggesting culturally mediated behaviour (**Paper IV**) and local adaptations (**Paper III**). State-dependent behaviour was also observed throughout the spawning season both at the school and individual level (**Papers III-VI**).

### 4.1 State-dependent behaviour on the school and individual level

#### 4.1.1 Horizontal dynamics

Herring stayed within the system throughout the study period, but there were significant differences in spatial positioning depending on the state of maturation (**Papers IV, VI**). During the pre-spawning period herring remained relatively stationary in a presumably safe place close to large depths (**Paper VI**). But when approaching spawning the horizontal dynamics increased with different individual timing of the migration towards the spawning location, which indicates conflicts among herring of different maturation state.

After spawning most herring were recorded closest to the outlet (**Paper VI**). Earlier studies have found that Lindås herring conduct feeding migrations to the outer basin after spawning (Østvedt et al. 1973) and migrate out of the main sill to the outside fjord system (Aksland 1978), but there is little information regarding the extent of this emigration. The lack of registrations at the main sill suggests that herring may utilize other inlets/outlets, possibly having changed their migration route, as

supported by the last registrations by a different receiver (**Paper VI**). In our study, there was thus no clear evidence of fish migrating out of the poll (**Paper VI**). **Paper II** suggests that Lindås herring has a faster growth as a result of migrating out of the system to more favourable feeding areas, and migration outside Lindåspollene is most likely the reason for the increase in growth of local herring after the 2000s. This assumption is consistent with Lindås herring mixing with NSS herring over an extended time period where they presumably join the young NSS herring migrating out of the system to feed outside (**Paper II**). There are two possibilities: 1) Herring remain within the study area, as the conditions within the system are satisfactory. Competition for food may however affect growth, condition and survival (Huse et al. 2012, Payne et al. 2012), depending on the amount of available zooplankton and the abundance of herring. However, if herring do not migrate out, they should maintain the same size (length) in the 1960s and 2000s, but in the 2000s Lindås herring became much larger, suggesting that they have migrated out, 2) Herring leave Lindåspollene after spawning. The reasons why they do not leave earlier could be good feeding conditions for a short period of time, or they may wait for other herring to complete spawning and reduce the predation risk by leaving in larger groups. This is based on that herring are capable of evaluating the size of their group that is cognitively demanding (Fernö et al. 1998). In order to clarify whether, when and where herring leave the system, we need to apply a larger number of receivers covering all possible inlets/outlets along with observing behaviour of tagged herring over a longer time.

#### **4.1.2 Vertical dynamics**

Herring conducted marked diel vertical migrations (DVMs) throughout the study period, but to a different extent over the spawning season (**Paper VI**). The DVMs were more extensive during the pre-spawning and ripe period compared to the shallow distribution both night and day during the spawning period. Herring normally descend at dusk to avoid predators (Levy 1987, 1990b, Clark and Levy 1988, Cardinale et al. 2003, Skaret 2007), which may explain why the herring stayed closer to the bottom during day time (**Paper VI**). Environmental factors may also affect fish



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behaviour (Mann & Lazier 1991). The majority of herring was not found in the surface layer prior to yearday 70 (**Papers IV, VI**) and seem to avoid temperatures below 3°C (Østvedt 1965, **Papers III, IV, VI**) and colder waters above sharp thermoclines in the pre-spawning phase (Langgård et al. 2006, Skaret 2007) that may influence the maturation of the fish (e.g., Hutchings & Myers 1994, Husebø et al. 2009, Jansen & Gislason 2011).

Herring generally ascend at dawn to forage (e.g., Cardinale et al. 2003, Eshenreder & Burnham-Curtis 1999), but herring do normally not feed until after spawning (e.g., Parsons & Hodder 1975, Crawford 1980, Huse & Ona 1996, Slotte 1999a) reflecting the change in trade-offs between reproduction and feeding (Nøttestad et al. 1996, Axelsen et al. 2000). Also herring in Lindåspollene generally had empty stomachs during the pre-spawning period (**Paper IV**). However, staying in shallow water could reduce gas diffusion through the wall of the swimbladder (Fässler et al. 2009). It has been suggested that herring are only able to inflate their swimbladder by ‘gulping’ atmospheric air at the sea surface (Brawn 1962, Blaxter et al. 1979, Blaxter & Hunter 1982, Blaxter & Batty 1984, Ona 1990, Nero et al. 2004), but we did not observe any surface visits prior to yearday 70 (**Paper VI**). A combination of energy conservation at shallow waters minimizing gas diffusion and avoidance of the risky surface waters during the day could explain the observed vertical dynamics.

As maturation progressed, herring gradually moved to the presumed spawning grounds while the differences in depth between day and night decreased, and herring gradually stayed higher up in the water column both during day time and night time (**Paper VI**). This change in vertical behaviour may be due to two reasons: 1) Closer to spawning, the warmer temperatures close to the surface could attract herring and speed up physiological processes, linked to maturation and spawning (Husebø et al. 2009) and 2) Herring accept the increased risk of staying closer to the surface when approaching spawning as they spawn in shallow waters. The latter was verified by egg deposition from the surface down to 15 m, although the occasional deep and long lasting dives (~ 40 m) could also represent spawning events (**Paper VI**).

### 4.1.3 School stability

Schooling fish are believed to make behavioural decisions to stay, join or leave a school (Pitcher & Parrish 1993). If there are several schools in the area, individuals may leave and join another school with individuals of more similar state and motivation. The degree of motivational synchronisation between individuals in a school will determine whether or to what degree a school split into multiple subgroups or remain integrated (Axelsen et al. 2000).

In general, the two herring components in Lindåspollene aggregated into one main school for several months in the pre-spawning period (**Papers IV-VI**) supporting the suggestion of the existence of a metapopulation in **Papers I & II**. There was, however, an interesting difference in behaviour at the school level (**Paper IV**) from what we observed on the individual level (**Paper VI**). **Paper IV** showed that the herring school was relatively stationary within a restricted small area up to two months prior to spawning, while **Papers V & VI** found that individually tagged herring split from and rejoined with the main school, demonstrating individual priorities of spatial positioning both vertically and horizontally during a phase of potentially conflicting interests. Around yearday 60 there was a drop in number of individuals at the pre-spawning area and an increase at the spawning grounds that could indicate a horizontal school split, with some herring migrating to the spawning area, while others stayed (**Paper VI**). However, the two components did not form any distinct groups, which suggest that they stayed together, in spite of the individual differences within the main pattern. With no schools in close proximity, motivational conflicts within a school can emerge as complex shapes and structures (Axelsen et al. 2000). Axelsen et al. (2000) observed a single herring school on a spawning ground splitting into one pelagic and one demersal component during spawning, suggesting conflicting motivations between ripe and immature herring. Johnsen & Skaret (2008) only observed this split in pre-spawning and post-spawning herring above spawning fish, and suggested that a school of individuals with conflicting motivations does not split below a certain threshold group size. A school split could have taken place in Lindåspollene, but the observations so far are better explained by individuals

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swimming back and forth between the receivers (**Paper VI**). If the school split, it would be interesting to see whether the herring then formed smaller groups made up of individuals with synchronized maturity state and if individuals from one of the components of herring present in Lindåspollene (**Paper I**) have a tendency to keep together.

#### 4.1.4 School structure

Packing density may provide detailed information about the internal structure of a school (Misund 1993, Gerlotto & Paramo 2003). The packing density increased in the late pre-spawning period (**Paper IV**). When approaching spawning, herring aggregated in a dense school close to the bottom (**Paper IV**) in accordance with earlier studies (Nøttestad et al. 1996, Mackinson 1999, Skaret 2007). High packing density is usually associated with anti-predator behaviour (Breder 1951) with fish seeking shelter in the school for protection (e.g., Hamilton 1971, Pitcher & Parrish 1993, Axelsen et al. 2001) and adhering more closely to conspecifics taking advantage of co-operative escape tactics (Pitcher & Parrish 1993). This could therefore represent precautionary behaviour in a riskier habitat at the bottom (Skaret 2007). In our study it was documented that herring encountered various predators, and in some cases had been preyed upon by large cod. Unfortunately it was not possible to quantify the predation pressure accurately due to irregular gillnet sampling (**Paper IV**).

The vertical extent of a school can reflect motivational differences between individuals within the school (Axelsen et al. 2000, Skaret 2007). The sampled herring showed various states of gonad maturation, with the Maturity Diversity Index (MDI) showing a peak around yearday 73 (**Paper IV**). This could result in conflicting motivation for vertical positioning within the school (Axelsen et al. 2000, Skaret 2007). Yet, in contrast to what is expected (Axelsen et al. 2000, Skaret 2007, Johnsen & Skaret 2008, Vabø & Skaret 2008) the vertical extent of the school appeared to decrease closer to spawning (**Paper IV**), and no vertical split was observed. This could suggest that attraction towards the bottom dominated in all fish.

Schools with a high MDI had higher heterogeneity in packing density (roughness) and remained closer to the bottom (**Paper IV**), which may reflect conflicts between individual fish at different stages of maturation. Because smaller schools as a result of higher packing densities have a larger proportion of fish at the edge compared to larger schools, this may influence the degree of positional changes of individuals within the school (i.e., O-turns, Domenici et al. 2002), and in this way affect roughness. In addition, a school with a high conflict level among the individuals should be expected to show a high roughness. The assumed increased conflict level did not seem to be strong enough to increase vertical extent, but the increase in roughness could still reflect conflicts between individuals of various stages of maturity (**Paper IV**). Individuals with high spawning motivation could also pull less motivated individuals in the school towards the spawning grounds (Reebs 2000, Huse et al. 2002, Skaret et al. 2003, Couzin et al. 2005) resulting in variable behaviour and increased roughness (**Paper IV**). Remaining within the school may be more important than optimising individual demands, illustrating how much individual herring in a school depend on each other, particularly when there are no other close schools to join in the area. In addition, predator interference could either stabilize or cause heterogeneity in packing density of the school: 1) when predators approach the school, individuals could become tightly packed, thereby decreasing roughness or 2) when predators attack, individuals closest to the predator could actively try to avoid them, thus increasing roughness.

#### **4.1.5 Timing and duration of spawning**

Based on the gonad maturation index, spawning commenced around yearday 80 (YD 77-97) with the main spawning taking place around yearday 90 (**Paper VI**). This is in accordance with the spawning peak found in **Paper IV**, and with the timing of spawning (**Paper III**). The spawning time in Lindåspollene was related to the rapid spring warming and thermal stratification regardless of variable ambient temperatures over the pre-spawning and spawning period (**Paper III**). This deviates from the general assumption that maturation rates and spawning time in herring is tightly linked to the ambient temperatures during the maturation phase (Haegele & Scheigert

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1985, Hay 1985, Winters & Wheeler 1996, Husebø et al. 2009, Óskarsson & Taggart 2009). The timing of peak spawning in many north-temperate stocks varies annually due to variation in ocean temperature (e.g., Lambert 1987). Warmer ocean temperatures affect the spawning time both in herring and other species (e.g., haddock; Page & Frank 1989, capelin; Carscadden et al. 1997) and could both advance and retard spawning (e.g., English sole; Kruse & Tyler 1983, Atlantic cod; Hutchings & Myers 1994). In addition, different herring populations have specific environmental preferences, which result in spawning at specific times and locations (Haeghele & Schweigert 1985). As a result, maturation rate increases with increased temperatures in herring, which probably is an adaptation to best match emerging larvae to available food in spring plankton blooms (Hay 1985, Ware & Tanasischuk 1989) in agreement with the match-mismatch hypothesis (Cushing 1990).

The local herring component in Lindåspollene could have adapted its maturation and time of spawning to the local conditions i.e., adapted a strategy to develop their gonads regardless of the ambient temperature and remain in the ripe maturity stage until the onset of thermal stratification (**Paper III**). In contrast to local herring, NSS herring spawning time is influenced by the temperature during overwintering (Husebø et al. 2009). Hay (1985) lists areas of Pacific herring with spawning time deviating from the main part of the population, and found that spawning time in some cases were affected by other factors than the temperature level, such as tides and time of day (Spratt 1981, Hay 1990), local weather conditions and ice break (Tyurnin 1973, Barton & Weststad 1981). Such variations are also observed in other species. Otterå et al. (2006, 2012) documented that under identical environmental conditions, different spawning time occurred among four local cod populations, presumably reflecting genetic interactions across local populations.

If oceanic and local herring are adapted to different cues for triggering maturation and spawning, this has interesting implications in a metapopulation context. Many local fjord populations of herring are assumed to belong to a metapopulation with an occasional exchange of genetic material with larger herring populations (Eggers 2013, **Papers I, II**). Adaptations to different cues for timing of spawning may

increase the threshold and hence decrease the probability for overlap in spawning. However, both components in Lindåspollene spawn simultaneously (**Paper II**) that is a requirement for exchange of genetic material. Although it is still not fully known which environmental or genetic factors that trigger spawning in local herring, the present study suggests that the local adaptation has prevailed in spite of the inflow of NSS (**Paper III**). The local herring “culture” and maturation state possibly involving schooling dynamics and pheromones (Scott et al. 1994) may have influenced NSS herring to join local herring to spawn. Whether NSS herring would spawn at the same time and location if local herring were not present remains unanswered.

Both individual and day-to-day variability in vertical positioning was high during the spawning period, with occasional deep daytime dives. Some dives lasted several hours and afterwards the herring was observed to migrate to the outer basin. This suggests that diving was associated with spawning. Spawning involves several trade-offs (Nøttestad et al. 1996, 2004, Sætre et al. 1998, Slotte & Fiksen 2000, Axelsen et al. 2000, Skaret et al. 2003), and the individual differences in timing of the dives may reflect different and changing individual behavioural motivations when approaching spawning (**Paper VI**). The actual spawning depth as well as the spawning duration was difficult to estimate. Herring have been reported to spawn during dark hours (Furevik 1976, Kjørsvik et al. 1990, Johannessen et al. 1995), and this is supported by evening surveys with no recorded eggs and observations of spawn the following morning (unpubl. obs). Spawning may, however, also take place during the day (Johannessen 1986, **Paper VI**). Overall, herring seemed mostly to spawn in shallow waters, from the surface down to 15 m depth (**Paper VI**), which is consistent with previous studies (Johannessen 1986, Jørstad & Pedersen 1986, Jørstad et al. 1994, Hay et al. 2001a).

#### **4.1.6 Evaluation of the acoustic methods**

**Papers I-VI** used an echosounder, with the sonar used as a supplementary method when conducting the acoustic surveys covering the entire system to detect other schools. The sonar was tested at the pre-spawning area, but data was not possible to

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utilize due to noise caused by shallow topography. For future studies, both sonar and echosounder should be applied simultaneously when studying herring schools in order to get a representative picture of the dynamics and to acquire a better basis for evaluating possible sources of error (Axelsen & Misund 1997). In most cases herring are observed to avoid surveying vessels, which may result in less representative observations of schooling behaviour (Axelsen & Misund 1997) and may introduce bias to acoustic abundance estimates (Olsen et al. 1983, Vabø et al. 2002). However, in the study reported in **Paper IV**, there was no relation between distance from the vessel to the school and school depth, as expected if the herring dove when the vessel came too close (unpubl. obs) as found by Olsen et al. (1983) and Axelsen & Misund (1997). In addition, comparisons between the echosounder on board the research vessel RV ‘Hans Brattstrøm’ and the individual acoustic tags (**Paper VI**) demonstrated that the herring were not affected by the vessel (unpubl. data). The RV ‘Hans Brattstrøm’ utilized in all studies has previously been shown to have negligible impact on herring behaviour (Axelsen et al. 2000, Skaret et al. 2005) and the local herring could also have habituated to the boat traffic over the years.

Echosounder recordings were only used during day time, but acoustic tags provided night time observations. In order to monitor the school without vessel interference and to examine the diel school dynamic patterns, we made some observations with a stationary echosounder, which was mounted on an aluminium rod attached to the rocks at the pre-spawning area in Lindåspollene pinging horizontally, as well as placing an underwater platform underneath the school pinging upwards during different years (Langård et al. 2008, Fatnes 2011). These observations showed that the herring school dissolved in the upper layers at night.

The success of tagging experiments depends on many factors, specifically handling and tagging mortality. The highest mortality is mostly due to the damage done to the fish when they are caught (Harden Jones 1968). Despite the fragility of herring, no mortality was observed in the days following tagging, but a few herring were classified as dead during the tracking period (prior to the start of March, yearday 60) (**Papers V, VI**). The behaviour of the remaining herring was interpreted as

representing natural behaviour (**Papers V, VI**). In **Paper V & VI** we attempted to avoid overlap between the acoustic receivers based on the pilot study (**Paper V**). The system was not calibrated with range-testing tags, and even though factors like bathymetry, shadow zones (Voegeli & Pincock 1996, acoustic telemetry) and distance to next receiver were considered when deciding the location of the receivers, there may have been some overlap in coverage between the two inner receivers.

These small-scale process oriented studies (**Papers IV-VI**) in different scales demonstrate how the individual state and of herring and the environmental conditions influence the overall schooling dynamics of herring. The chain from individual behaviour to ecosystem dynamics can be monitored on fine time-scale, providing the possibility to test concrete hypotheses.

## **4.2 A metapopulation perspective**

### **4.2.1 Spawning overlap between different components of herring**

The overlap in maturity stages 6 (running) and/or 7 (spent) between the two components of herring found in Lindåspollene indicated that they spawned at the same time (**Papers I, II**), which is a requirement for existence of a metapopulation (McQuinn 1997a). Together with the presence of both components in the same school, this strongly indicates mixing during spawning. The consistency in length throughout the maturation period also indicates that the larger NSS herring stay in the study area throughout spawning supporting that local and NSS herring interbreed in Lindåspollene (**Paper II**). Yet, as long as the cross-fertilization between herring could not be directly observed one cannot exclude that the components might separate during the actual spawning event. Detailed data is needed to confirm this and there is still no documentation of genetic contributions in the offspring from different components. We did not observe other spawning locations during the studies, but further investigations are needed to find possible alternative spawning grounds.

Few studies have observed spawning between different components within a marine species. Jørstad & Pedersen (1986) demonstrated that juveniles from the NSS herring



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population were found in the pelagic while the local population was at the bottom in the same fjord in Balfjord in northern Norway. Knutsen et al. (2011) found that coastal Atlantic cod may be represented by two separate populations; one residing in the inner, sheltered part of a fjord, where it appears to complete its life cycle, whereas a larger population genetically resembling the North Sea cod stock occupies the skerries outside the fjord.

#### **4.2.2 Changes in the components of herring in Lindåspollene**

The inflow of NSS herring in Lindåspollene seems already to have started prior to the collapse in the late 1960s (Fig. 1). At this point in time there were clear differences between NSS and local Lindås herring. Two modes could be distinguished at ages 3-4 with one component consisting of small herring with low VS and another component of larger herring with higher VS (**Papers I, II**). Low VS and slow growth characterize local herring populations along the Norwegian coast (Broch 1908, Runnström 1941a, Aasen 1952, Jørstad & Nævdal 1981, Jørstad & Pedersen 1986, Hognestad 1994, Sørensen 2012, Eggers 2013). The second component was interpreted as oceanic NSS herring, based on the higher mean VS (>57) and rapid growth (Holst et al. 2004). From VS, otolith and fish scale analyses it was found that young fish (3-4 years old) belonged to a mixture of local and NSS herring and old fish mainly to the local herring population (5-11 years old) (**Papers I, II**). The clear differences in meristic characters (**Paper II**), suggests that there has been little overlap between the NSS and the more stationary local populations prior to the collapse when the NSS stock levels were high and the overwintering, spawning and feeding areas expanded over larger areas (Devold 1963, Dragesund et al. 1980, 1997, Røttingen 1990, Slotte & Dommasnes 1998, 1999, Slotte 1999b). Spawning then took place on the offshore banks. The majority of the larvae would thereby drift directly northwards towards the Barents Sea, but a small proportion of the larvae also end up in the coastal and fjord nursery areas from 58-71°N (Dragesund 1970a, Holst & Slotte 1998).

VS were crucial to separate the components. VS are primarily determined by environmental factors during embryogenesis (Parlov & Shardin 1998) and should

therefore identify geographical origin of different herring components. We assume that both genetic and environmental factors contribute to VS, although the relative significance of the two factors remains unclear. Still, there is consensus that the variation is directly affected by the environmental conditions at the spawning grounds and early development (Tåning 1952, Hempel & Blaxter 1961, Lindsey 1988). Temperature is negatively correlated with VS, whereas salinity has the opposite effect (Hempel & Blaxter 1961, Lindsey 1988). Herring hatched in the fjords and under different inshore environmental conditions will have lower VS, whereas younger, larger herring in the fjords with high VS would typically be a result of NSS herring larvae hatched offshore and later drifted into the fjords (**Paper II**). This is consistent with past studies (Tåning 1952, Harden Jones 1968, Hulme 1995, Johnston et al. 1997), and indicates that the differences in VS are a result of hatching at different spawning grounds (Runnström 1936).

After the collapse, juvenile NSS herring in the Barents Sea were rare and mostly confined to the warmer fjord waters (Dragesund et al. 1997, Holst & Slotte 1998), where they outnumber the small coastal herring populations (Engelhard & Heino 2004b). Most NSS herring are believed to migrate out when they are 1-2 years old, but some NSS herring growing up in the fjords may choose to spawn there (first time or multiple times), instead of migrating out to the Norwegian Sea adopting the adult stocks mode of life. Herring growing up on the coast, not undertaking oceanic migrations in the 1970-80s would likely mix with and utilize similar spawning areas as the local populations, and thereby end up spawning in a similar environment, yielding similar VS (**Paper II**). During the 1970-80s, both young and old herring of the fast growing and slow growing components (**Paper II**) had low VS with no clear indications of the oceanic NSS herring component. The more stationary NSS herring may have contributed to establish a coastal NSS herring population with low VS, as found in local herring, but with a similar size (length) to NSS herring (in particular among young herring, **Paper II**). VS in herring of more than 4 years of age were relatively constant over time, while VS of younger herring changed markedly over time, suggesting a stronger influence of NSS herring. In **Paper I**, the strange

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component with lower VS was not classified as NSS herring, but this was based on otolith analysis that did not allow for a correct classification of young fish. In light of the results acquired after analysing the historic data the strange herring was interpreted as a mixture of NSS herring with high VS and local Lindås herring with low VS.

Two strong year classes (1983 & 1988) allowed the stock to rebuild in the late 1980s and 1990s (Dragesund et al. 1997). After the recovery, the slow growing component with low VS more or less disappeared and was replaced by a fast-growing component with low VS (**Paper II**). This is in accordance with significant amount of mixing with NSS herring with the main increase in length-at-age taking place in the 1970s to the 1990s year classes. Because the older fish had low VS we suggest that relatively few old oceanic NSS herring were present after migrating out after a certain age (**Paper II**). Some coastal NSS could also be present but these could not be separated from fast growing local herring.

Overall, in the 1960s there seemed to be a mix between local and NSS herring of 2-4 years. In the 1970s, after the collapse, the low VS suggested that the oceanic NSS herring were absent, and in the 2000s, VS increased again in 2-4 year old herring. Hence the decrease and subsequent increase in VS matches the decline and rise of the oceanic NSS herring population (**Paper II**), which is consistent with the changes in growth, size, and age in the local herring. Local herring matured at a larger size after the collapse compared to the 1960s, and attained a similar size as the NSS herring in the 2000s (**Paper II**). Looking at the “big” picture, the variations in NSS herring abundance resulted in herring moving from the ocean to the coast and back to the ocean.

#### **4.2.3 Traditions influencing connectivity between components**

The role of traditions in the Lindås herring, in terms of adaptation and homing behaviour, is indicated by the consistent aggregation during a period of six years into one main school (**Paper IV**), at the same location as in the late 1970s (Aksland 1983, Johannessen 1986), in spite of an increased size and the inflow of another component.

Aggregating over a long time might have permitted the local Lindås herring to persist as a “cultural” population, adapted to the local conditions despite prolonged mixing with NSS herring (**Paper III**). Although the spawning location varied from year to year, they were always in close proximity to the pre-spawning area (Furevik 1976, Lie et al. 1978, Aksland 1983, Johannessen 1986).

An alternative explanation as to why herring aggregate at the same site every year could be that this specific location is a preferred place irrespective of culture. The pre-spawning area in Lindåspollene is characterized by a trench that leads directly to the deepest basin, suggesting that herring in Lindåspollene have adopted a precautionary approach by staying in a place that provides an escape route to deeper waters (**Paper IV**). Herring have been reported to hide in deep trenches close to the spawning grounds to avoid visual predators (Runde 2005, Skaret 2007). Pacific herring schools in British Columbia have also been found to form strong associations with dips in the seabed (Mackinson 1999) to reduce predation risk (Lima & Dill 1990, Magnhagen 1993) and further conserving energy through hydrodynamic advantage. In addition, by remaining relatively stationary within a limited area, herring spend little energy, and the steep sidewall at the pre-spawning area could also function as a meeting point (Fréon & Dagorn 2000, Castro et al. 2001, Fish Aggregation Devices) or reference point to guide migrations of herring to and from the spawning grounds. All the same, the preferred conservative strategy of herring (Fernö et al. 1998, Corten 2002, Huse et al. 2010) may have stabilized the choice of the pre-spawning area in Lindåspollene.

The local herring increased both in growth and condition over time (**Paper II**), suggesting that the NSS herring may have initiated a change in migration strategy of the local herring (McQuinn 1997b). The probability of overlap with local herring increased when the NSS herring remained at the coast throughout the year, and directed movements of NSS herring could strongly influence the movement of the entire school (Huse et al. 2002). The dominating component of strong NSS herring year classes may have influenced some local herring to join the school and vice versa (**Paper II**), in accordance with past studies (Fernö et al. 1998, Corten 2002, Huse et

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al. 2002), thereby generating a change in migration behaviour (**Paper VI**). Interbreeding with migratory NSS herring may also have strengthened the migration tendency, with local herring realizing their genetically increased growth potential. The herring may emigrate out of the poll after spawning, as the final registrations were detected in the outer basin closest to the outside fjord system (**Paper VI**) consistent with past studies (Østvedt et al. 1973, Aksland et al. 1978). Earlier tagging studies in Lindåspollene found that herring migrate out, but are unclear as to which component of the population the recaptured fish belonged to (Dahl et al. 1973).

As both components originally had two different “traditions” in terms of migratory and stationary strategies, they could have a mutual influence on each other; Lindås herring may have influenced NSS herring to spawn at specific times and locations, whereas NSS herring may have influenced Lindås herring to take advantage of the resources in the outside system, resulting in a higher migration tendency.

According to the adopted-migrant hypothesis (McQuinn 1997a) migration routes are learned and adopted by young and first-time spawning herring (i.e. recruit spawners) as they join older and more experienced spawning herring (i.e. repeat spawners) (Dodson 1988, McQuinn 1997a, Slotte 1999b, Huse et al. 2002, 2010, Kerr et al. 2010). In North Sea herring populations, transmission of migration patterns by learning has been suggested to play a key role in maintaining population identity (Wynne-Edwards 1962, Corten 1993), as well as across a range of species (clupeoids, tuna, striped bass, whiting, Petitgas et al. 2010). While mixing provides an opportunity for connectivity, persistent schooling allows for maintenance of integrity (Stephenson et al. 2009). Once a fish has adopted an initial migration trajectory, population persistence may be reinforced by learning and social interaction (Krause & Ruxton 2002, Kerr et al. 2010, Petitgas et al. 2010), which may be what is observed in Lindåspollene (**Papers I, II, IV**).

Traditions will continue until, for example, a year class could lack the guidance normally provided by the older herring or a larger proportion of recruits dominate the population (Corten 2002, Huse et al. 2002, 2010, Petitgas et al. 2010). Traditions are

suggested to play a role in Lindåspollene as to why herring return to the same pre-spawning area every year (**Papers II, IV**). We cannot prove that the same individuals return to this area every year, but it is likely as this pattern has prevailed for over three decades (Lie et al. 1978) and herring have a tendency to spawn on the same spawning grounds in successive years (e.g., Pacific herring; Hourston 1982, Atlantic herring; Wheeler & Winters 1984a). In the tagging experiment, one acoustic tag was recovered at the same location after two years (unpubl. obs). A tendency towards returning to spawn at specific spawning grounds could secure a spawning location with suitable environmental conditions with regard to bottom substratum and temperature (Slotte & Fiksen 2000).

Rose (1993) described how aggregations of migrating cod were organized by size and age classes, and how this type of organization could facilitate learning migration routes. Schooling further demands a certain degree of size-matching among individuals (Pitcher et al. 1985) and young NSS could join schools made up of similar sized fish (**Paper I**) of both young and old local herring, and thereby adopt their migration patterns and behaviour within the same system (**Paper II**).

#### **4.2.4 Life history traits**

Life history traits under selection to maximize fitness (McQuinn 1997a, Sterns 1976, Wootton 1998) and heritability of life history traits are quite large (Roff 2000). Prior to the collapse there were clear differences between NSS and local herring indicating specific life history tactics (**Paper II**). Local herring were originally characterized by a slow growth and a short life span, whereas marine migratory species, including NSS herring, generally grow faster, become larger and mature later and at a larger size (Roff 1988).

NSS herring perform extensive migrations in the Norwegian Sea, and large size is then crucial as the energy loss during migration decreases with size (Slotte 1999a). In contrast, the Lindås herring is believed to be relatively stationary with low migration costs that imply a different allocation between body growth and reproduction. Allocation of resources into high fecundity is traded off against somatic growth and

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survival (Burton et al. 2010), and the trade-off between growth and reproduction is usually strong in herring (Runnström 1936, Engelhard et al. 2003). According to life history theory, Lindås herring should thus be expected to invest more in reproduction, and the reproductive effort in the 2000s was markedly higher than that of NSS herring (Silva et al. 2013). Different adaptations exist with regard to reproductive investment, including large differences in size- and age-at-maturity among individuals and female investment in egg production with substantial variability both among and within populations (Fleming 1996).

Fish have limited energetic resources and there are trade-offs between somatic growth, survival and reproduction (Roff 1983, Stearns 1992). In South American characin (*Protilodus mariae*) a trade-off between migration costs and reproduction was documented, where stationary females allocated five times as much energy to egg production compared to females performing up-river migration (Saldana & Venables 1983). However, such a trade-off does not seem to occur in Lindåspollene in the 2000s, instead, short migrations to outside productive waters Lindås herring could provide more resources with low energy costs and thereby combine rapid growth with high reproductive effort (**Paper II**). A high investment into reproduction is only achieved by taking higher risks (Jørgensen & Holt 2013), which could explain the initial short life span of Lindås herring.

After the collapse, the local component gradually became a more long-lived, fast-growing fish such as the NSS herring (Dragesund et al. 1980). The local herring also increased the length at first maturity by about 3 cm from the 1960s to the 2000s (**Paper II**), whereas NSS herring show no plasticity in length at first maturity, in spite of large changes in density and environmental forces (Engelhard & Heino 2004b). This suggests that interbreeding has changed genetically determined life-history traits. Such changes in life history traits in local Lindås herring have not been observed in Trondheimsfjorden (Sørensen 2012) or Lusterfjorden (Aasen 1952 and unpubl. data), suggesting that these areas are more isolated than and thus not as influenced by NSS herring as the local herring in Lindåspollene.

Herring is known as a flexible species with a high level of adaptability (Geffen 2009), and the flexible life history enhances the adaptability to respond to environmental change. The food availability does not seem to have been improved for herring in Lindåspollene (**Paper II**) so this does not explain the increased size of local herring. However, NSS herring known to adjust feeding migrations to areas with abundant food (Dragesund et al. 1980, Broms et al. 2012) could above a certain size approach a size-dependent growth limit and migrate to more productive waters (**Paper II**) outside Lindåspollene and thereby generate migrations in local herring, resulting in faster growth. It is less clear how a plastic response to changes in food could explain the increase in age, but faster growth in combination with a size-dependent mortality (Duffy & Beauchamp 2011) may influence longevity.

The change in life history traits could be the result of phenotypic plasticity, genetic responses or a combination of the two (see also Amundsen et al. 2012). Rapidly fluctuating environments may favour flexibility and plasticity, whereas longer fluctuations may favour the evolution of enhanced evolvability (Lee & Gelembiuk 2008). However, the changes in life history traits observed in Lindåspollene might be the result of genetic mixing rather than selection, as an increased inflow of NSS herring resulting in mixed spawning could change several traits of the local herring. Changing a population of slow growing fish with small length at maturity and a short life to become a fast growing, long living fish that mature at larger size does not happen overnight. Whether genetic or cultural changes explain what has taken place in Lindåspollene is yet to be determined and we might be witnessing the start of a more long lasting selection process that in fact possibly can reverse the process by an adaptation to the local environment in Lindåspollene. For example, individuals of the freshwater fish vendace (*Coregonus albula*) colonized a new habitat responded within a few generations with changes in numerous life history traits with large size and low mortality replaced by small size, high mortality and earlier reproduction (Amundsen et al. 2012).



## 5. Implications for management

Currently there is a lack of knowledge regarding the genetic diversity of local herring populations along the Norwegian coast, making management plans difficult to implement. Today we know only about a few of the many potentially unique populations with phenotypic adaptations to a stationary way of life among the wide range of Norwegian fjords/bays with a potential connectivity with NSS herring (Husebø et al. 2005, Eggers 2013, **Papers I, II**). These relatively stationary populations could contribute to the biodiversity along the coast. It is central to understand the population composition of harvested fish as well as the dynamics in order to avoid overexploited populations and to improve the guidelines for the conservation and management of biodiversity and stock preservation of local herring populations and ecosystems.

Understanding the spatio-temporal dynamics and persistence of fish aggregations is an important first step to developing appropriate models of the potential consequences of management actions (Wright et al. 2006). The degree of connectivity between population components and the persistence of these components over time are vital to our understanding of the origin of observed population structure (Svedäng et al. 2007, Secor et al. 2009). Higher rates of connectivity through straying and entrainment will affect the internal metapopulation dynamics with regard to persistence and stability (Secor et al. 2009). Understanding the connectivity patterns identifying periods with high/low connectivity is essential for predicting the likely genetic impacts on local populations. Kell et al. (2009) simulated the long-term management plans of a metapopulation and demonstrated that lumping of different populations will underestimate the risk of a collapse and overestimating the probability of recovery. Management strategies have been suggested in order to stabilize metapopulations (Secor et al. 2009) and Stephenson et al. (2001) was the first to consider stock sub-units in management (e.g., survey, assess, then fish protocol) taking into account both the spatial and temporal distribution. Regardless of whether Atlantic herring is qualified as forming a metapopulation, understanding spatial-dynamics is a priority both for population

conservation and fisheries management. Likewise, a decline in the abundance of Atlantic cod might be associated with the loss of both spawning individuals and areas (Stephenson 1999), hence spawning time and areas must be preserved under a precautionary approach.

The findings of this thesis challenge the concept of discrete local populations in line with the accumulating evidence that Atlantic herring populations form one or several metapopulations and suggest that local populations can act as a buffer at low stock levels and permit a more rapid recovery of the former dominating stocks, thus contribute to new recruitment and increase the integrity and persistence. Ask yourself how long it would take for a stock to recover if there were no coastal herring? Information about the spatial structure of populations, intermixing and the ecology and life history dynamics of individual populations is essential in order to develop sound fisheries management.

## 6. Future perspectives

More research effort should be put forward in studies of the spatial and temporal distribution of local herring populations along the Norwegian coast to fully understand their dynamic interactions with NSS herring and recognizing their true value to improve the advice, management and conservation. Regular assessment of for example the population size, demography, connectivity and genetics (Jones 2006) is needed to determine the local population size and degree of mixing as the boundaries between the distributional range is unclear and variable along with utilizing the extensive and existing information from historical studies of local herring populations along the Norwegian coast comparing past and present catches (i.e., historical growth data from different coastal populations, mixing at spawning locations, homing-specific affiliations, habitat characteristics).

The results and suggestions of this thesis require further investigations and systematic studies of change in age structure over time, otolith shape (Burke et al. 2008) and microstructure (Clausen et al. 2007), core microchemistry (Hatfield et al. 2005), and stable isotope composition (Valle & Herzka 2008), as a supplement to the studies of microsatellite DNA of offspring (McPherson et al. 2004, Bekkevold et al. 2005, Mariani et al. 2005, André et al. 2011, Teacher et al. 2013) and SNPs (Lamichhaney et al. 2012, Limborg et al. 2012, Nielsen et al. 2012, Corander et al. 2013). This should further improve our understanding of herring population structure and enable us to track the ontogenetic history of individual herring identifying and separating local and oceanic herring populations.

Our results are mainly based on VS and suggest that VS from the different components can indicate specific environmental conditions under which fish eggs were incubated and consequently stock identity. However, as the origin of herring in Lindåspollene and the influence of environmental conditions needs to be clarified, rearing experiments with hybrids between different herring populations under different environmental conditions indicating origin (Folkvord et al. 2009), both with regard to eggs and larvae, should also be performed. A pilot study on the genetic

stock identification of herring in the northeast Atlantic using microsatellite DNA found genetic differences between Lindås and NSS herring along with other populations along the Norwegian coast as well as herring populations in the Norwegian Sea (Skirmisdóttir et al. 2012). Considering how environmental factors affect population connectivity and patterns of population genetic structuring can also benefit management and conservation efforts (White et al. 2010).

In order to verify whether different populations stay or leave after spawning, acoustic tagging experiments should be conducted. A large-scale acoustic monitoring system covering large parts of the Norwegian coast year round, tracking herring migration routes after spawning in the local areas, offers another way to study linkages between fish populations. Furthermore, identifying the geographic origin of the different herring components, applying x-ray, ultrasound methods or other technology (e.g., photo technique) to screen individuals for VS, length, age and condition could reveal their identity without harming the fish. Tagging experiments on herring from the larval-juvenile stage would provide information on where they reside within the system (inside/outside polls) essential with regard to retention areas. To increase the resolution of the spatial dynamics even further, stationary positioning systems (VRAP) that track the positions of each fish in real-time may be employed. Combining information on the micro and meso-scale behaviour will make it possible to address basic ecological questions about the schooling dynamics of pelagic fish. Parasites could also be applied as biological 'indicators', 'tags' or 'markers' of stock boundaries, recruitment, migration and mixing of marine (Williams et al. 1992, MacKenzie 2002), anadromous and freshwater fish (e.g., Brooks et al. 1981, Bérubé & Curtis 1986, Bailey et al. 1988). Parasites as markers permit identification of both discrete stocks and linkages between different life history stages as marine fish migrate over long distances from or to spawning and feeding areas (Bailey et al. 1988, Lester 1990, Mosquera et al. 2000). Finally, a growing body of evidence reveal that many fish populations are responding to climate change in a variety of ways (Johannesson et al. 2011, Fincham et al. 2013), and this element needs to be considered when managing different components of commercially exploited species.

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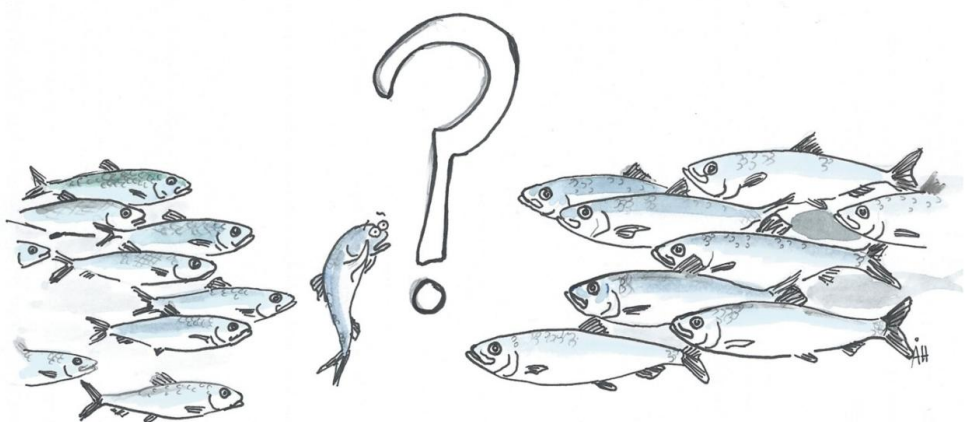


Illustration: Åse Husebø



# Two components of Northeast Atlantic herring within the same school during spawning: support for the existence of a metapopulation?

Arne Johannessen, Leif Nøttestad, Anders Fernö, Lise Langård, and Georg Skaret

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It has been hypothesized that some stocks of Atlantic herring are subject to genetic exchange and therefore should fit the definition of a metapopulation with subunits. Genetic exchange requires spatial overlap of individuals from different populations during spawning. We investigated a local herring population that is assumed to feed and spawn within the semi-enclosed marine ecosystem of Lindåspollene in west Norway, which is connected with the outer fjord only by a narrow sill. Acoustic recordings and gillnet samples demonstrated the mixed presence of two components within a single school throughout the spawning period 2005–2007. Members of the two components were of about the same size and in a similar stage of gonad development at all times, but the age composition was completely different. These observations represent the first documented case of different components being present in a spawning school and provide strong indications of regular interbreeding. Our data suggest that the two components represent autochthonous Lindås herring and allochthonous herring of coastal/oceanic origin, thereby supporting the metapopulation concept. Two alternative explanations, based on one migratory and one resident component of a single Lindås stock, are also discussed.

**Keywords:** *Clupea harengus*, interbreeding, maturity, metapopulation, Northeast Atlantic herring, population structure.

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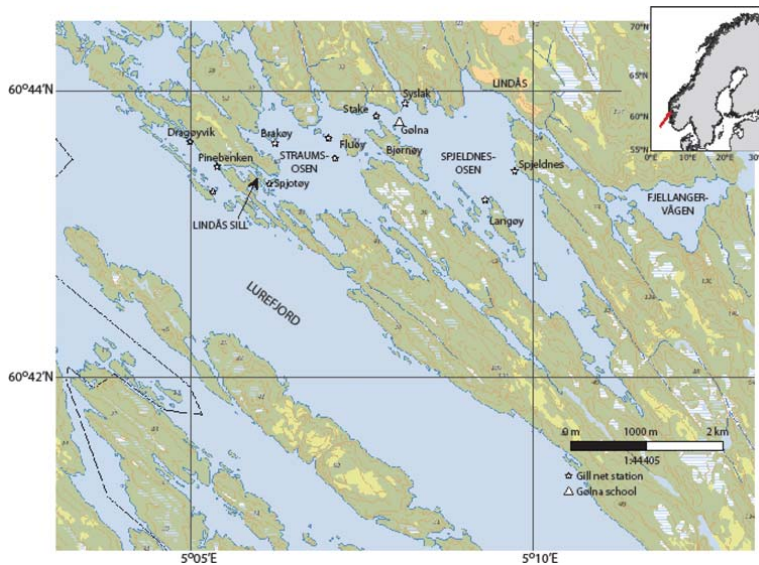
## Introduction

Animal species often comprise multiple populations that are reproductively isolated and can be distinguished based on morphological, physiological, behavioural, and/or life-history traits, or most convincingly, by genetic analyses (Hanski and Gilpin, 1997; Wilson, 1999). A population composed of two or more distinguishable subunits with variable but moderate interbreeding is defined as a metapopulation (Levins, 1969, 1970). In the past few decades, the metapopulation concept has become widely and firmly established in terrestrial population and conservation biology (review by Hanski and Gilpin, 1997), and to a lesser extent in marine science (McQuinn, 1997; Grimm *et al.*, 2003; Kritzer and Sale, 2004). However, as Kritzer and Sale (2006) state: “The metapopulation concept is here to stay in marine ecology. Science demands it, fisheries management needs it, and it is the last hope for marine conservation”.

Considerable debate surrounds the issue of population structure and reproductive exchange between subunits of marine fish populations (Iles and Sinclair, 1982; Ruzzante *et al.*, 2006). The Atlantic herring (*Clupea harengus*) has a highly complex population structure, and various stocks often exhibit variation in spawning season, genetic structure, and life-history parameters (Clausen *et al.*, 2007). The Atlantic herring is geographically

isolated and genetically distinguishable from the Pacific herring (*Clupea pallasii*; Grant, 1986; Domanico *et al.*, 1996), and it has been divided into separate stocks based largely on major geographical barriers between spawning locations or phenotypic differences (Heincke, 1898; Hulme, 1995; Jørgensen *et al.*, 2005, 2008; Bekkevold *et al.*, 2007), including spawning time. In a few cases, these stocks have been demonstrated to be genetically distinct: for example, some spawning groups in the Northwest Atlantic (McPherson *et al.*, 2004), as well as the Balsford herring in the Northeast Atlantic, which appears to be more closely related to the Pacific herring than the Atlantic herring (Jørstad *et al.*, 1994; Shaw *et al.*, 1999). For many stocks, however, it has not yet been possible to establish genetic distinctions (Hauser *et al.*, 2001). McQuinn (1997) suggests that the gene flow between many herring stocks may be sufficient to define them as belonging to the same metapopulation, with some local population integrity maintained through specific larval retention areas and behavioural isolation involving homing to specific spawning areas.

No clear evidence has yet been obtained for interbreeding of herring stocks—a principal requirement for the classical metapopulation concept (McQuinn and Lefebvre, 1995; McQuinn, 1997). The herring is a pelagic schooling species that spawns demersally in synchronous waves (Skaret *et al.*, 2003).



**Figure 1.** Map of the Lindåspollene area in west Norway, with location of the main School at Gølna (triangle) and gillnet sampling locations (stars).

A prerequisite for the existence of metapopulations is the occurrence of a temporal and spatial overlap during spawning that allows genetic exchange between subunits. Spring- and autumn-spawning populations of herring in the Northwest Atlantic have overlapping distributions before spawning, but the schools split up during their respective spawning times (McQuinn and Lefebvre, 1995; Overholtz *et al.*, 2004; Stephenson *et al.*, 2009). Although there may be some connectivity between these populations (through mixing of juveniles on the nursery grounds), individuals marked during spawning have only been recaptured at the spawning ground where they were tagged (Wheeler and Winters, 1984; Hay *et al.*, 2001). Norwegian spring-spawning herring (NSSH) undertake extended migrations from feeding areas in the Norwegian Sea and overwintering areas to spawn along the Norwegian west coast (Dragesund *et al.*, 1980; Johannessen *et al.*, 1995; Fernö *et al.*, 1998), where several smaller local populations of herring, which do not participate in long-distance migrations, are also present. Spatial overlap between these local populations and NSSH during the spawning period has, however, not been documented. There is also little information on how stationary the local populations are, and whether they interbreed.

Our study focuses on a small local herring population in Lindåspollene that is regarded as distinct from NSSH because of its deviating growth pattern and smaller size-at-age (Lie *et al.*, 1978). This population has been present for several millennia in a semi-enclosed marine system that is characterized by a limited scope for exchange with the outer sea via a narrow sill (Johannessen, 1986; Langård *et al.*, 2006). The aim was to quantify the spatial and temporal overlap of local Lindås herring with herring of a different origin before, during, and after spawning, based on established methods in fishery biology.

## Material and methods

### The Lindåspollene ecosystem

Lindåspollene is a small ( $\sim 7 \text{ km}^2$ ) well-defined ecosystem in west Norway (Figure 1). A narrow sill (7.5 m wide, 3.5 m deep) leads from the Lurefjord into the enclosed fjord system, which comprises three distinct, 60–90 m deep basins. Between the first basin (Straumsøsen; maximum depth 60 m) and the second basin (Spjeldnesøsen; maximum depth 90 m), there is a sill 5–10 m deep (Aure, 1972). The third basin (Fjellangervågen; maximum depth 75 m) is anoxic from  $\sim 18 \text{ m}$  deep to the bottom, and adult herring have rarely been observed there. A general description of the topography, hydrography, and the diverse biota of Lindåspollene is given in Dahl *et al.* (1973). The environment within the basins differs from that of the Lurefjord with regard to temperature, salinity, and oxygen, as well as to species abundance, species assemblages, and diversity of food items (Dahl *et al.*, 1973; Lie *et al.*, 1978). The local Lindås herring is generally not commercially exploited and represents a key species in terms of ecological importance (Langård *et al.*, 2006).

### Research vessels and instrumentation

Two research vessels were employed. The RV “Hans Brattstrøm” (24.3 m long and 6.5 m wide; 79 GRT) was equipped with Simrad EK60 (38 kHz) and Simrad EQ55 (50 kHz) echosounders for recording of fish and for bottom detection. A Kaijo Denki KCH-1827 (163 kHz) multibeam sonar was used for exploratory surveys of fish aggregations. The RV “Fangst” (14.98 m long and 5.5 m wide; 25 GRT) was equipped with Simrad EK60 (38 kHz), EK500 (38 kHz), and Skipper GDF 201 echosounders. Gillnet sampling of herring and its potential predators was carried out

**Table 1.** Summary information for the herring samples collected from Lindåspollene, 2005–2007 [locality, see Figure 1; distance of sample location from the main school; category, see explanation in text; mesh size—B, bottom gillnet, and F, floating gillnet; *n*, number of herring caught; (*n*), subsample size, if applicable].

Year	Date	Locality	Distance (m)	Category	Mesh size (mm)	<i>n</i>	( <i>n</i> )
2005	23 February	Fluøy	1 000	Far field	34 B	131	–
	23 February	Gølna	0	School	34 B	50	–
2006	25 February	Gølna	0	School	34 B	49	–
	22 February	Gølna	0	School	34 F	73	–
	22 February	Gølna	0	School	29–34 B	14	–
	24 February	Gølna	0	School	31–34 B	71	–
	24 February	Gølna	0	School	34 F	247	(82)
	01 March	Gølna	0	School	29–34 B	224	(94)
	24 March	Spjotøy	1 250	Far field	34 F	20	–
	24 March	Gølna	0	School	34 F	3	–
2007	09 January	Syslak	400	Nearfield	29 F	20	(15)
	10 January	Syslak	400	Nearfield	29 F	52	–
	14 February	Fluøy	1 000	Far field	34 F	23	(18)
	15 February	Pinebenken	2 500	Far-field-out	30 F	11	–
	15 February	Dragøyvik	3 500	Far-field-out	30 F	9	–
	15 February	Stake Bjørnøy	400	School	29 F	16	–
	17 February	Gølna	0	School	29 F	2	–
	20 February	Gølna	0	School	29 F	24	–
	21 February	Lurefjorden	3 000	Far-field-out	30 F	1	–
	27 February	Gølna	0	School	34 F	38	–
	05 March	Stake Bjørnøy	400	Nearfield	29 F	13	–
	05 March	Brakøy	1 750	Far field	29 F	2	–
	07 March	Gølna	0	School	29 F	9	–
	08 March	Gølna	0	School	29 F	30	–
	15 March	Syslak	300	Nearfield	29 F	5	–
	20 March	Gølna	0	School	29 F	22	–
	20 March	Syslak	300	Nearfield	29 F	19	–
	27 March	Brakøy	1 750	Far field	29 F	14	–
	27 March	Syslak	400	Nearfield	29 F	42	–
	29 March	Brakøy	1 750	Far field	29 F	8	–
	29 March	Gølna	0	School	29 F	4	–
	29 March	Syslak	400	Nearfield	29 F	9	–
	03 April	Syslak	400	Nearfield	29 F	10	–
	03 April	Gølna	0	School	29 F	15	–
	12 April	Syslak	400	Nearfield	29 F	12	–
	12 April	Gølna	0	School	29 F	15	–
	17 April	Gølna	0	School	29 F	3	–
	24 April	Gølna	0	School	29 F	20	–
	24 April	Syslak	400	Nearfield	29 F	31	–
	24 April	Brakøy	1 750	Far field	29 F	13	–
	02 May	Syslak	400	Nearfield	29 F	10	–
	09 May	Gølna	0	School	29 F	17	–
	09 May	Syslak	400	Nearfield	29 F	2	–

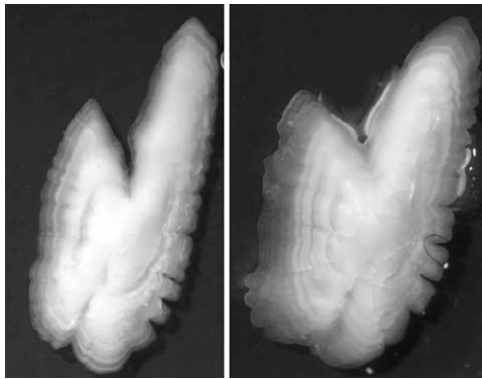
from a small boat (Vernøy 430 SL) with a 15-hp engine. A portable high-resolution and wide-angle SIT (Silicon Intensifier Target) underwater camera was used to record exploratory films of the bottom substratum and herring spawn. In addition, scuba divers inspected the spawning grounds in 2006. An instrumental platform (Langård *et al.*, 2008) equipped with a Simrad EK60 (120 kHz) echosounder was installed on the bottom below the prespawning herring school (at ~30 m) during the field season.

### Biological sampling

For comparative purposes, gillnet sampling was conducted within a radius of 100 m around the midpoint for the school (category School), between 300 and 400 m from the midpoint for the Nearfield, and at least 1000 m from the midpoint of the Far field. Sampling effort increased from 2005 to 2007, with the

greatest effort spent in the School area. Herring samples were obtained at the surface (5 m) and near the bottom using monofilament gillnets (29–34 mm mesh) during January–April in 2005–2007. The nets were set based on local knowledge of the herring distribution, aided by acoustic detections (Figure 1). In 2007, mostly the 29-mm mesh was used (Table 1). Larger mesh (57–79 mm) monofilament gillnets and entangling nets were set to catch potential predators on herring and herring eggs (e.g. cod, pollack, and haddock) and to verify time and place of spawning. The nets were usually set in the afternoon (17:00–19:00) and hauled the next morning (9:00–12:00), after a soak time of 14–17 h. An overview of the number of herring caught is given in Table 1.

Samples were frozen and transported to the laboratory for further analysis. No correction has been made for shrinkage



**Figure 2.** Typical otoliths from: (left) a C2 herring, with clear annuli in the grey zone; and (right) a C1 herring, with more diffuse annuli along the edges.

caused by freezing. Individual herring were analysed with regard to total length, total body weight, sex, vertebrae counts, stomach content, maturity stage, and gonad weight. Eight maturity stages (Mjanger *et al.*, 2007) were distinguished, based on macroscopic visual inspection of the gonads: 1, immature; 2–5, maturing or prespawning; 6, spawning; 7, spent; and 8, resting stage. Age was determined from otoliths and/or fish scales by experienced age readers.

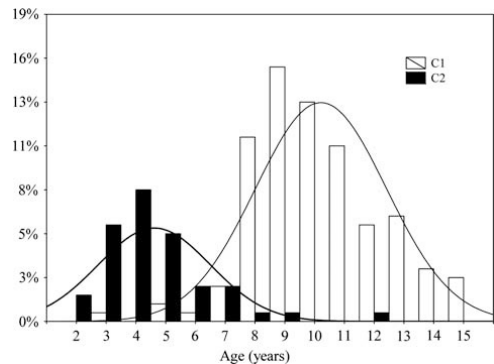
### Classification of components

Individual herring were classified as representing one of two components (C1 or C2), based on a set of criteria applied in a sequence of categorization steps. First, one otolith reader (with more than 30 years of experience of readings from various herring stocks in the Northeast Atlantic) classified the herring based on otolith appearance (percentage unclassified was ~10%). Second, a comparison was made between the appearance of otoliths and scales to identify a common set of criteria. Subsequently, a sample of otoliths and scales from the same fish ( $n = 119$ ; 2007 material) was read by two independent experts. Third, a subset of the otoliths collected ( $n = 44$ ; 2007 material) was analysed morphometrically using three metrics of otolith shape that appeared to differ between the components. These three metrics were combined into a model describing the ratio of the length of rostrum ( $R$ ) relative to the length of the antirostrum ( $A$ ) multiplied by the cosine of the angle between the antirostrum and rostrum ( $\alpha$ ), as measured at the vertex at the core [ $R(A \cos \alpha)^{-1}$ ]. For the measurements, "ImageJ" (Abramoff *et al.*, 2004) was applied to otolith photographs taken using light microscopy (Figure 2). Finally, the numbers of vertebrae of all herring were counted.

## Results

### Schooling behaviour

Several (<5) smaller schools were present in Lindåspollene during all years of investigation, but >80% of all herring detected acoustically were observed in a main school, which was present at the same location (Gølna) each year. The school became less dense at night, but did not disperse, based on continuous diel acoustic



**Figure 3.** Age–frequency distribution (%) by component within the main School at Gølna in spring 2007.

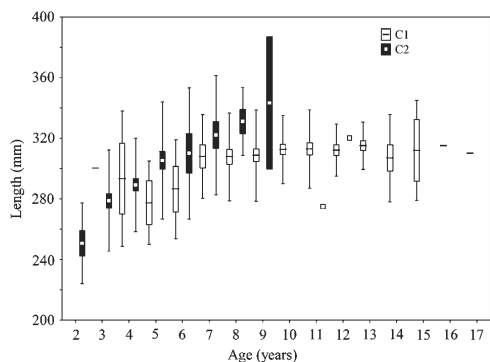
recordings by echosounder and multibeam sonar. Its spatial midpoint generally moved within an area of ~200 m<sup>2</sup>.

### Classification

Several criteria were used to discriminate between the two components (C1 and C2). Otoliths of herring older than 4 years were assigned to C1 if they were characterized by a grey region with no annuli or with only very diffuse opaque zones along the dorsal edge between the antirostrum and post-rostrum, whereas those with distinct opaque annuli in the grey region were assigned to C2 (Figure 2). These differences in the otoliths matched specific patterns in the ring structure laid down in the scales, and the sample of otoliths and scales taken from the same fish showed agreement in the classification by two independent age readers in 88% of the cases. Although showing considerable overlap, the morphometric model, based on three metrics, indicated a highly significant difference between the two components (Kolmogorov–Smirnov,  $n = 44$ ,  $p < 0.001$ ) that proved to be independent of age (Kruskal–Wallis,  $p > 0.05$ ). Finally, the vertebrae counts, although highly variable (range: 54–59), supported the classification based on otoliths, with herring classified as C2 yielding significantly ( $p < 0.01$ ) higher counts than those classified as C1 (mean  $\pm$  s.d., 56.75  $\pm$  0.95 vs. 56.52  $\pm$  0.77, respectively).

A Silverman test (Silverman, 1981) revealed that the overall age–frequency distribution of the samples collected in 2007 was clearly bimodal. These modes coincided with the peaks in the age distribution of the two components (Figure 3), thus yielding further support to the classification criteria used. The C2 fish were on average much younger than the C1 fish. Also the length-at-age (all samples from the start to the end of the spawning period combined; i.e. 14 February–9 May 2007) differed markedly with, on average, the C2 fish having a consistently larger length-at-age than the C1 fish (Figure 4). No C1 fish younger than 4 years were recorded in the samples, whereas the C2 component was represented by fish aged from 2 years and upwards.

The mean length of the C2 fish did not differ between stations, but slight differences were found for the C1 fish (ANOVA,  $p = 0.03$ ). When pooled over all stations, the fish in C1 were larger than those in C2 (mean  $\pm$  s.d., 31.0  $\pm$  1.5 vs. 29.3  $\pm$  2.3 cm, respectively; Welch two-sample  $t$ -test,  $p < 0.0001$ ). The largest



**Figure 4.** Mean total length (mm), s.d., and 95% confidence interval vs. age (years) by component within the main School at Gølna in spring 2007.

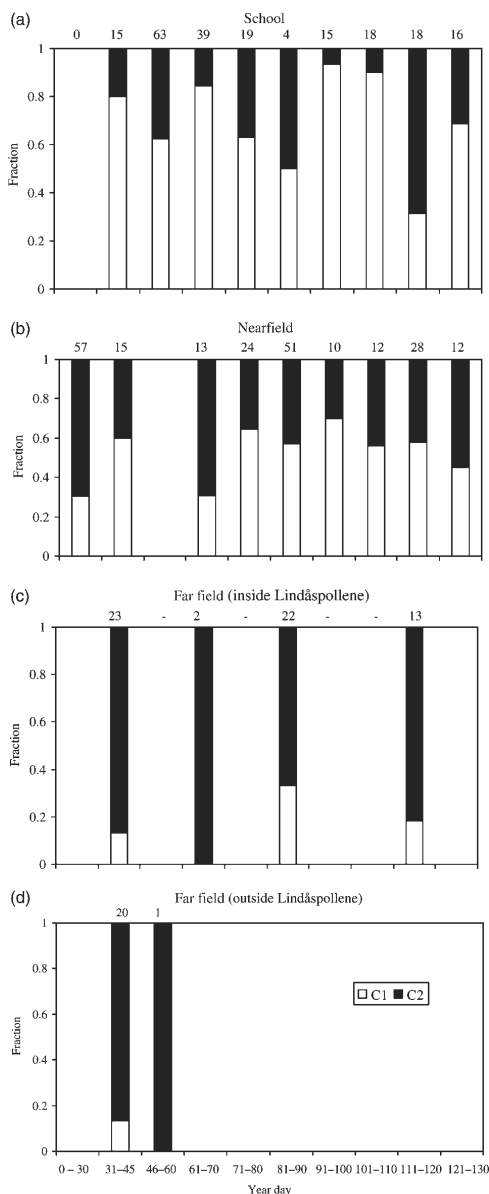
herring recorded in 2007 in Lindåspollene was a 36-cm C2 herring. No significant effects of fishing depth or mesh size were found. Herring of a similar size to those caught in gillnets were also found in the stomachs of cod (*Gadus morhua*) and pollack (*Pollachius pollachius*).

As not all age groups are represented in the two datasets, a statistical comparison of the overall growth curves was considered inappropriate. Instead, we compared length-at-age for those age groups represented by at least one individual from each component (2007, pooled over all stations). Applying a regular Welch two-sample *t*-test, we found C2 fish to be significantly larger than C1 fish at ages 5 ( $p < 0.005$ ), 6 ( $p < 0.01$ ), 7 ( $p < 0.01$ ), and 8 years ( $p < 0.0001$ ). No differences were found for 4-year-olds (few C1 data) and 9-year-olds (few C2 data). The C2 fish had therefore grown faster from hatching than the C1 fish.

Herring belonging to the two components were found together not only in the same area, but also repeatedly within the same school (Figure 5). The C1 component was generally larger than the C2 in the School (Mann–Whitney *U*-test,  $p < 0.01$ , 2007 data), whereas the C2 was predominant in the Far field ( $p < 0.001$ ), both inside and outside of Lindåspollene. No difference was found in the Nearfield. In 2007, only one (out of 21 fish) C1 herring was caught outside the sill at Dragøyvik (Figure 1).

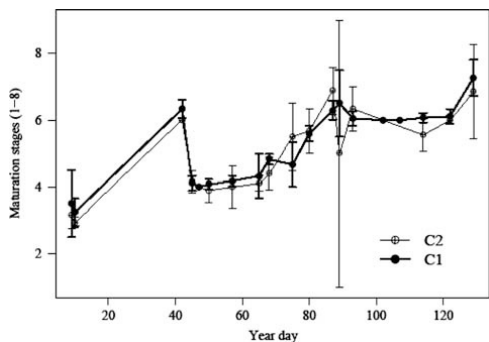
**Maturity**

In 2007, prespawning herring were present both inside and outside Lindåspollene by January. C1 and C2 herring exhibited virtually the same pattern in terms of mean maturity stage for each sampling date in all years (linear regression model for 2007:  $r^2 = 0.84$ , d.f. = 16,  $p < 0.0001$ ; Figure 6). Spawning within Lindåspollene was confirmed by several additional observations in 2007: (i) visual observations of egg layers on 28 March; (ii) samples of herring spawn in haddock stomachs on 7 and 24 April; and (iii) aggregations of diving common eider (*Somateria mollissima*) near Gølna on 23 April. Observations of two spent C2 herring as early as 15 February, just outside the sill, indicate an extensive spawning period, but based on the occurrence of prespawning and spawning maturity stages, the main deposition of eggs was estimated to take place from 20 March on for both components (Figure 7).

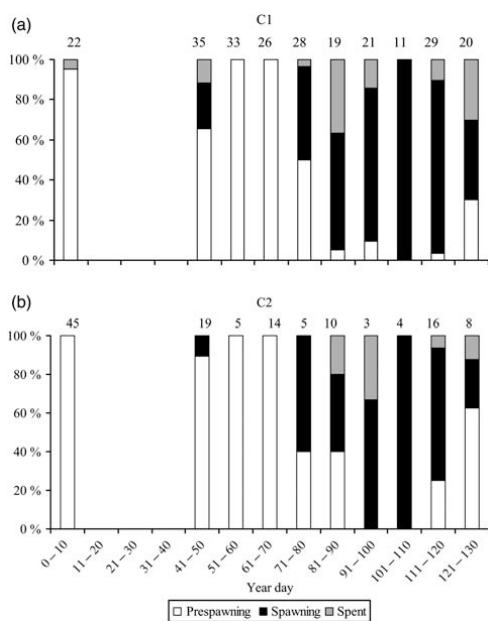


**Figure 5.** Proportion of C1 and C2 herring caught in gillnets by year day (2007 only; number of fish classified given at the top) and category: (a) School; (b) Nearfield; (c) Far field inside Lindåspollene; and (d) Far field outside Lindåspollene.

Based on samples from local fishers, both components were still present in Spjeldnesosen (Gølna, Syslak, and Spjeldnes) during the feeding season in September–October of 2005–2007, whereas the



**Figure 6.** Development of the mean maturity stage ( $\pm 2$  s.e.) for the two components by year day (2007 School and Nearfield samples only).



**Figure 7.** The percentage of herring in different stages of gonadal condition (prespawning, including maturity stage 8; spawning; and spent) in 2007 by year day for (a) C1 and (b) C2.

size and age range had not changed from those observed during the spawning season. The C2 component comprised  $\sim 15\%$  of the fish sampled in September 2005 (total sample  $n = 110$ ).

## Discussion

Based on otolith analyses, vertebrae counts, and age structure, there is convincing evidence that the main school in Lindåspollene during the pre- and spawning period has two components. Most data presented are from 2007, but the

additional information available suggests that this situation has existed for all three consecutive years (2005–2007). Although the two components were about the same size, with very similar maturation patterns, one component was significantly younger and had reached a larger size-at-age. Fish in spawning condition as well as spent fish were observed among both components, suggesting that they spawn jointly on the same ground at the same time. Although one component dominated numerically within the school, both components were found together in all but one of the samples taken. This appears to be the first observation of the presence of more than one component within a single spawning school of herring. However, it is by no means certain how this observation should be interpreted.

## Lindås herring and immigrant herring

If we assume that the two components represent true Lindås herring and immigrants originating from the outside marine environment, the component in which the age distribution shifted to the older ages (C1) is interpreted as representing Lindås herring, and the other (C2) as representing immigrants because C1 herring were rarely present in the Far-field samples and only 1 of the 21 herring caught outside the sill was classified as C1. This suggests that the C1 component is predominantly confined to Lindåspollene, although there may be occasional straying (Lie and Dahl, 1981). The immigrants are assumed to enter Lindåspollene and join the Lindås herring to spawn. The absence of older C2 herring in the samples and their higher length-at-age suggest that only individuals in the appropriate size range join the spawning school. This selection for the younger age groups of immigrants may be based on their size. Schooling demands a certain degree of size-matching among individuals (Pitcher *et al.*, 1985), which is related to the unequal swimming power of siblings of different size (Nøttestad *et al.*, 1999) and the effective anti-predator behaviour of schools (Nøttestad *et al.*, 2002). The difference in vertebrae counts between the two components confirms earlier observations, made during the 1970s (Lie *et al.*, 1978); it also supports the assumption of a different population origin, because the number of vertebrae is primarily determined during the embryonic stage in response to environmental conditions, such as temperature (Johnston *et al.*, 1997; Pavlov and Shadrin, 1998), which may be expected to differ among spawning areas (Lie *et al.*, 1978).

The adopted-migrant hypothesis (McQuinn, 1997; Corten, 2002) postulates that first-time spawners that join another population adopt the behaviour of its members. C2 fish have also been caught in Lindåspollene during the feeding season in September–October, suggesting that some immigrants remain in the system after spawning. The two C2 individuals that were aged 11 and 12 years, with a length-at-age comparable with the C1 fish (Figure 4) may represent immigrants that have adopted the stationary way of life of true Lindås herring. Naive fish originating from mixed breeding may also adopt the behaviour of local herring and therefore be indistinguishable based on phenotypic characteristics.

What is the population origin of the immigrants? The C2 otoliths were originally classified as representing NSSH. However, the mean vertebrae count for pure NSSH is higher than that observed for the C2 component (57.0 vs. 56.75; Runnström, 1941; Lie *et al.*, 1978). Moreover, the large variation indicates that the C2 component represents a mixture of spring-spawning populations of oceanic and/or local coastal populations.

### Resident and migratory Lindås herring

If we assume, instead, that the two components represent Lindås herring with different life histories, then all fish in the spawning school represent one and the same "Lindås" population, which happens to be split into a resident component (C1) and a migratory component (C2). Any distinguishing features would therefore be completely phenotypic. Such a split may be caused by larval drift and retention mechanisms, with the different morphometric characteristics determined entirely phenotypically by the local environmental conditions experienced by the two groups. For example, temperature (Folkvord *et al.*, 2004) and food abundance (Johannessen *et al.*, 2000) influence otolith growth (Gallego *et al.*, 1996) so there may be mixing of subpopulations (Limburg, 1998; Brophy and Danilowicz, 2002; Valle and Herzka, 2008). A strong homing mechanism could bring the migratory component back to Lindåspollene to spawn with their natal population. The bimodal age distribution observed might then be explained by different trends in year-class strengths of the two groups or by widely divergent mortalities. In the absence of any information on these aspects, we explore two other mechanisms that might cause a bimodal age distribution.

Let us first consider the possibility that the migratory component only returns to spawn in Lindåspollene until it has outgrown the resident component. Based on the same size-selective forces within schools discussed above, the older age groups might join schools made up of herring in a more appropriate size range that originate from other populations and spawn outside Lindåspollene. This second explanation would, in fact, be the reciprocal of the first explanation, so also supporting the metapopulation concept.

The third explanation assumes that the migratory component will gradually cease to migrate outside of Lindåspollene and hence eventually mix completely with the resident component. As a consequence, the otolith and scale characteristics typical of the migratory component might become blurred, and the absence of older age classes in the migratory (C2) component would have to be explained by our inability to recognize them as a separate group. Although the migratory component might mix with other populations during the feeding season, there is not necessarily any connectivity in a genetic sense (Stephenson *et al.*, 2009). Therefore, this explanation does not support the metapopulation concept.

### Interpretation

Although the last two explanations could account for the differences in phenotypic expression, such as otolith appearance and growth rates among the two components, the difference in the vertebrae counts supports the first explanation. The vertebrae are formed at very early stages (Pavlov and Shadrin, 1998) and should therefore reflect the origin of the fish at spawning. In addition, the last two explanations cannot adequately explain the bimodality in the age–frequency distribution because they presuppose processes that would involve gradual and related changes, rather than abrupt and independent changes, in the age distribution of each of the two components. Therefore, we suggest that the explanation of a local component and a component of immigrants is the most likely.

Cross-fertilization between herring from the two components, a prerequisite for gene flow, could not be observed directly. Alternatively, the two components might separate during the

actual spawning events. However, this seems unlikely because of the highly synchronous maturation pattern and the restricted movements of the school. Although experience (for instance first-time vs. repeat spawners) might have some effect, a similar size is probably a more important criterion for spawners than age in selecting appropriate partners to associate with during spawning. The size–frequency distributions clearly show a considerable overlap in terms of means and standard deviations. Separation of the individuals during the actual spawning event according to their population origin would therefore require currently unknown abilities of kin recognition in herring. Non-random associations between individual herring have been reported, but these may be explained by long-term school cohesion (Hay and McKinnell, 2002). Although interbreeding cannot be proven unequivocally, our results provide a strong indication of genetic exchange between different components of the Norwegian stocks of herring, at least in terms of mating. A genetic exchange demands further that larvae from mixed breeding are viable. Folkvord *et al.* (2009) show that the eggs of North Sea autumn-spawning females fertilized by NSSH males produced viable larvae during the post-feeding stage. Therefore, it would seem unlikely that different populations of only spring spawners would meet difficulties in this respect.

### Conclusions

Our results indicate that the local Lindås herring population interbreed with herring originating from the outside marine environment, and they can therefore be regarded as a population within a metapopulation, characterized by a weak migration tendency. Extensive overwintering, spawning, and feeding migrations of NSSH seem to be culturally transmitted between generations (Corten, 1999, 2002), as modelled by Huse *et al.* (2002). The important role of traditions in the Lindås herring, in terms of adaptation and homing behaviour, is indicated by the consistent aggregation during the three years into one main spawning school at exactly the same location as in the late 1970s (Dahl *et al.*, 1973; Aksland, 1983; Johannessen, 1986). Such behaviour might have permitted local herring to persist as a "cultural" population, possibly with some adaptations to the local conditions (Bekkevold *et al.*, 2005), in a semi-enclosed coastal ecosystem, yet forming part of a larger metapopulation. The three explanations given are not mutually exclusive, and the actual situation may be even more complex.

The population structure of herring is complicated and has been a challenge for scientists for decades. Our conclusions challenge the concept of discrete local populations in line with the accumulating evidence that Atlantic herring populations form one or several metapopulations (McQuinn, 1997). Systematic studies of changes in the age structure over time, analyses of otolith shape (Burke *et al.*, 2008), microstructure (Clausen *et al.*, 2007), core microchemistry (Hatfield *et al.*, 2005), and stable isotope composition (Valle and Herzka, 2008), as a supplement to the studies of microsatellite DNA of offspring (McPherson *et al.*, 2004; Bekkevold *et al.*, 2005; Mariani *et al.*, 2005), might enable us to track the ontogenetic history of individual herring, identify possible hybrids, and resolve the population structure in a metapopulation context.

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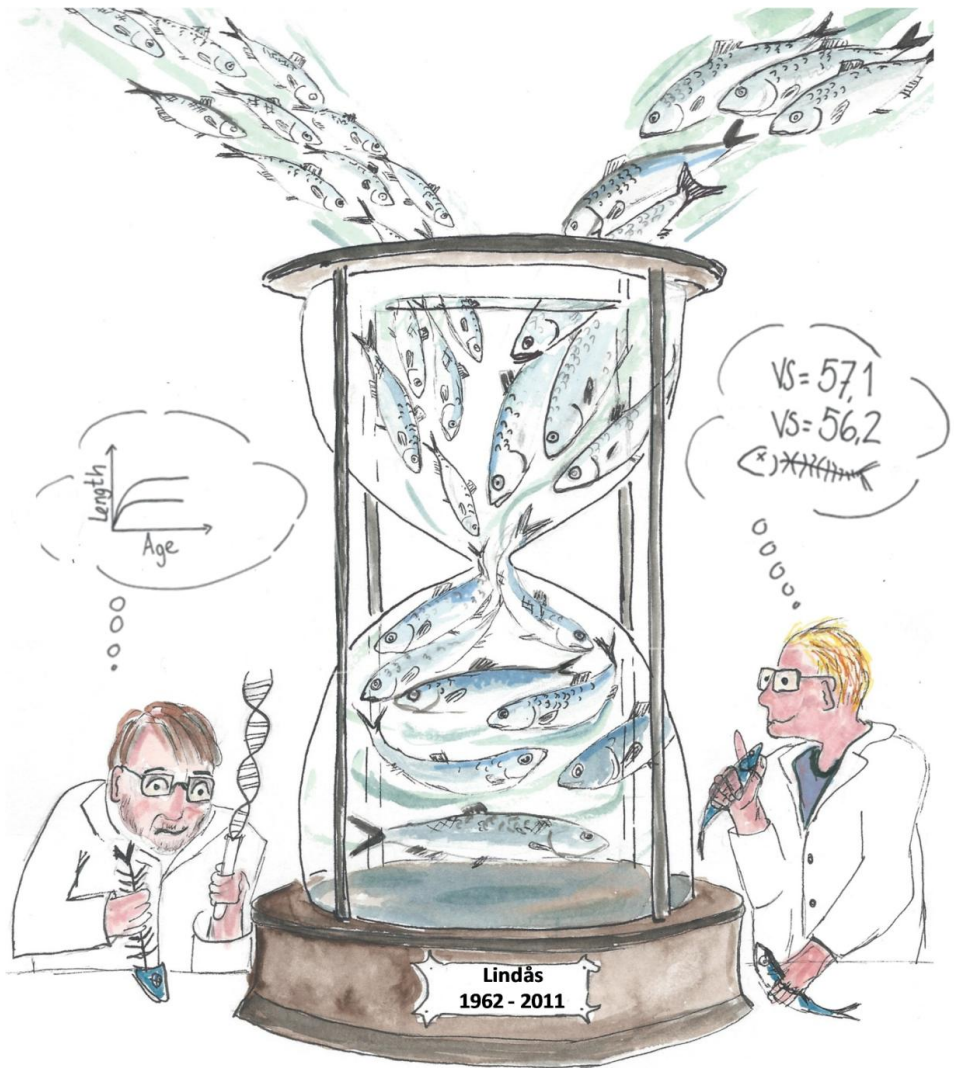


Illustration: Åse Husebø

# **The dynamics of a metapopulation: changes in life history traits in local herring following increased connectivity with oceanic herring**

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## **ABSTRACT**

Few fish populations have been covered over a sufficiently long time to reveal the temporal dynamics of the subpopulation structure. We aimed at elucidating the potential for genetic exchange between different components in Atlantic herring in relation to historical and recent changes in population size and distributional patterns. In a semi-enclosed coastal marine ecosystem in south-western Norway a small local herring population was sampled by gillnets during three periods in 1962-2011. During these periods, the Norwegian spring spawning (NSS) herring component underwent marked changes since the large, migrating and oceanic component collapsed, resulting in a more stationary behaviour closer to the local coastal populations before a subsequent recovery to the migratory, oceanic state followed. Different components were identified by the growth patterns and mean vertebrae counts (VS). One component with slow growth and low VS occurring in the 1960s was interpreted as local herring, and another component with rapid growth and high VS only present until age 4-5 was interpreted as oceanic NSS herring. Also in the 1970s and the 1980s one slow growing and one rapid growing component were present, but both components now had low VS and were interpreted as local herring and coastal NSS herring. Finally, in the 2000s both components showed rapid growth but one had low VS and one high VS and they were interpreted as local herring and oceanic NSS herring. The size, age, and size at maturity of the local herring increased markedly over time. There was an overlap in spawning time between the components supporting mixed spawning, and the relative importance of genetic and cultural factors behind the changes in life history traits is discussed. The distributional shift of NSS herring resulting in increased connectivity with local herring demonstrates that the relationship between components of Atlantic herring can be highly dynamic.

KEYWORDS: Herring – Spawning – Two components – Historical data – Mean vertebrae count – growth - maturation

## INTRODUCTION

The Atlantic herring (*Clupea harengus*) is often called "population rich" because of its complex population structure [1]. Numerous ecologically and morphologically divergent stocks classified as sub-species, races, tribes etc. have been recognised on both sides of the North Atlantic [2]-[4]. The Atlantic herring is geographically isolated and genetically distinguishable from the Pacific herring (*Clupea pallasii*) [5], [6]. Also within Atlantic herring a low but significant genetic structure has been found between some spawning components [7]. The spatially explicit genetic structure in the well-studied North Sea-Baltic Sea area [8-11] provides evidence that a significant degree of reproductive isolation is maintained over ecological and evolutionary time scales [7]. The genetic structure in this area is presumably the result of interplay between environmental factors influencing for instance larval retention, behavioural traits such as natal homing and demographic processes [5], [12]. Still, the degree of reproductive isolation and genetic differentiation between the different subunits of Atlantic herring is not completely resolved.

A metapopulation is a set of populations with variable but moderate interbreeding between the subunits [13], [14]. Atlantic herring is widely distributed, but the gene flow between the different subunits is believed to be sufficient to define them as belonging to the same metapopulation [15]. Different components often mix on feeding and wintering grounds [11], [16], [17], but genetic exchange between subunits of a metapopulation requires spatial overlap during the spawning period.

A number of spatially segregated local herring populations exist along the Norwegian coast [18]-[22]. In the semi-enclosed coastal marine ecosystem in Lindåspollene in south-western Norway the presence of a local herring population as well as a strange component has been documented since 1962 [20]. Johannessen et al. [23] observed that local herring and a strange component with a similar maturation pattern occurred together in a pre-spawning school in Lindåspollene, providing some support for genetic exchange between different components of herring. Atlantic herring are renowned for large variations in life history traits [24], and the local populations including the herring in Lindåspollene seem to have evolved different traits than the highly migrating oceanic component of Norwegian spring-spawning (NSS) herring

and are generally characterized by slower growth, a shorter life span and higher relative fecundity [19],[ 20], [22], [25]-[28].

The demographic dynamics of local populations are strongly dependent upon local processes, but are also influenced by external replenishment [29]. Estimating rates of interpopulation exchange is thus crucial. Range expansions and changes in the use of spawning locations have been reported for several herring stocks in the North Atlantic following fisheries-induced population collapses [30].

The spawning stock of NSS herring dropped from more than 10 million tonnes in the 1940-50s to near extinction in the early 1970s [31] and increased to full recovery in the late 1980s [24]. During this period the migration pattern changed from oceanic to coastal and back to oceanic [32]. In the 1950s, NSS herring had feeding and wintering grounds in the Norwegian Sea. Spawning occurred off the Norwegian coast from Møre (NW Norway) and southwards [31]. After the stock collapse, the remaining herring stayed along the coast throughout the year overwintering in fjords in NW Norway and spawning more inshore [33], [34]. After 1986, feeding migrations into the Norwegian Sea resumed [34]. Spawning areas gradually expanded northwards, and the herring now overwintered in fjords in northern Norway [33]. Hence, after the collapse the majority of NSS herring grew up along the coast and not in the Barents Sea [32] and remained in coastal waters to feed and spawned more inshore than before the collapse [33]-[35]. This distributional shift brought NSS herring closer to the local populations along the coast [32].

The dynamics between different population components, such as local and oceanic herring, can be studied by different methods [36]. Genetic studies can provide valuable insight in the population structure of herring (e.g., [7]), but the frequently used microsatellite DNA is unable to detect population differences in phenotypic plasticity, or norms of reaction, for fitness-related traits [37]. Furthermore, molecular methods usually only consider contemporary samples providing a “snapshot” of the genetic composition (but see [38]). No information about possible variations over time and the factors behind these variations is thus obtained. There are several interlinked factors that could influence the genetic exchange; changes in migration patterns could influence to what extent different components come into contact and the size of the subunits could influence the migratory behaviour. Employment of historical samples is crucial to understand the dynamics of the population structure [39]. For

the local Lindås herring there is a time series of data (1962-2011) on growth pattern and vertebrae counts in a period extending from pre-collapse to post-recovery of NSS herring. Such data have the potential to separate local herring and any NSS herring occurring in Lindåspollene in a period of extremely variable abundance and distribution of the main oceanic herring component. In a previous study [23] the strange herring in Lindåspollene were classified as different from NSS herring based on the appearance of the otoliths, but a closer examination has shown that this analysis does not permit a correct classification of young fish.

Our objectives were to investigate whether a distributional change in a large oceanic highly migratory herring stock to become more coastal “bound” influenced a local herring population. We wanted to evaluate the potential for genetic exchange between these subunits by examining the co-occurrence and maturation stages of the fish and to study whether interbreeding over time changed the life-history traits of the local herring.

## **MATERIAL AND METHODS**

### **The Lindåspollene ecosystem**

Lindåspollene is a small (~7 km<sup>2</sup>) semi-enclosed ecosystem in south-western Norway comprising of three 60-90 m deep basins (see [20]), with a main sill (7.5 m wide, 3.5m deep) connecting to the outside fjord. The environment within the basins differs from that of the outside Lurefjord with regard to temperature, salinity and oxygen [20], [40], and the zooplankton biomass in the basins is generally lower [41] and the size of the copepods smaller [42]. The local Lindås herring is a key species in the system [20] and are generally protected from harvesting [43].

### **Biological sampling**

Biological gillnet samples of herring were obtained from 1962 to 2011 in three periods 1962-1964, 1970-1982 and 2005-2011 (see Table 1). Length and weight were recorded for nearly all fish and age for the majority of the fish. Meristic analyses (vertebrae counts, VS) were conducted throughout the period but with a low effort in the 1970s.

Herring were sampled with 25 m long by 4 m deep gillnets of mesh size 26 mm. The exceptions were 1979-1980 and 2005-2011 when mesh size ranged from 21 to 31mm and 19-



36 mm, respectively. Samples were taken throughout the year but mainly in February-April. The nets were set at the surface in two of the basins (Spjeldnesosen and Straumsosen) based on local knowledge of fish distribution, aided by acoustic detections. The nets were usually set in series of three at 17:00-19:00 local time and hauled the next morning (09:00-12:00).

Subsamples of maximum 200 herring were kept for further analyses (see Table 1).

Herring were sampled for total length (nearest 0.5 cm below), total body weight (W), age, maturity stage and VS onboard the vessel or frozen immediately after capture and later sampled in the laboratory. Age was determined from scales until 1982 and thereafter mainly from otoliths by experienced age readers. Eight maturity stages were distinguished based on macroscopic visual inspection of the gonads; 1-2, immature; 3-5 maturing or pre-spawning; 6, spawning/running; 7, spent; and 8, resting stage [44]. VS are primarily determined by environmental factors during embryogenesis [45] and should therefore identify geographical origin of different herring components. Fulton's condition factor K [46] was calculated as:

$$K = 100 \cdot \frac{W}{L^3}$$

### **Data analyses**

We compared basic population parameters (age, age and length at first maturity, length and condition factor) of herring between the three sampling periods, where the first coincides with the period prior to the collapse of the NSS herring (P1, 1960s, year classes (YCs): 1950-60s), the second with the period during the collapse (P2, 1970-80s, YCs: 1960-1970s) and the third with the period after the recovery (P3, 2000s, YCs: 1990s-2000s). In cases where the population parameters were normally distributed (length and weight), a regular ANOVA with a Tukey HSD post-hoc test was applied to compare between periods. In the case of age, the non parametric Kruskal-Wallis-test was used. The herring sampled during the three periods contained YC from five different decades (1950s, 1960s, 1970s, 1990s and 2000s) for which selected population parameters could be compared independently of annual variability in sampling effort. Such parameters included growth measured as length-at-age and VS. In order to investigate growth patterns at the start and end of the period studied, the von Bertalanffy growth function = VBGF [47] was fitted to length-at-age data from the YCs of the 1950 and 2000 decades. All statistics were performed using R version 3.0.0 (R Development Core Team 2013, <http://www.rproject.org>).

## RESULTS

### Analyses of the whole time series

In the 1960s to 1980s the samples consisted of herring with age only up to about 10 years (Figure 1). There were then some predominant YCs that could be followed for up to 11 years. The 1969 YC could for instance be followed from age 2 (1971) to age 12 (1981). From 2005 no single, predominant YC could be clearly followed over time, and from 2007 the age range became wider and older herring (up to 20 years) were more frequent.

### Variations in population parameters over time

There was a significant increase in age, length, weight and condition factor from P1 to P3 ( $p < 0.001$ , Table 2). Notably, mean age and weight approximately doubled from the 1960s to the 2000s.

Age at first maturity did not change over the 50 years (Figure 2a); in all periods the herring started to mature at age 2 and close to 100 % had matured at age 3. In accordance with the increasing size over time, the length at first maturity increased from a situation where close to 100 % were maturing at the length of 22-25 cm in the 1960s and 1970s to a situation where less than 20% were maturing at this length in the 2000s (Figure 2b).

### Identification of different components

Figure 3 provides the length at age as a proxy for growth for the YCs of the 1950s, 1960s, 1970s, 1990s and 2000s. The growth pattern changed over time. Two growth curves were fitted with the von Bertalanffy Growth Function (VBGF), one based on the length-at-age data from the 1950s (slow-growing, red curve superimposed in Figure 3) and one based on data from the 2000s (fast-growing, green curve). The latter curve had a steeper increase ( $k=0.49$  versus  $0.22$ ) and reached the asymptote at a higher level ( $L_{\infty 2000 YCs}=329$  versus  $L_{\infty 1950 YCs}=310$ ) than that of the 1950s. Notably, there were components of the young age groups (mainly 3-4 years old) in the YCs of the 1950-70s with a length-at-age fitting better with the VBGF for the 2000s than for the 1950s, indicating that some fast growing individuals were present as young but later left the area. On the other hand, few specimens were observed among the 1990-2000s YCs that fitted well with the slow growing 1950s VBGF. There was an increased length-at-age with decadal period (ANOVA of age groups 6-9 (sufficient N from all decades),  $p < 0.001$ ) (Figure 4) with the main increase taking place between the 1970s and the 1990s.

Since gillnets with different mesh sizes were used in the 1960s and the 2000s the effect of net selectivity was investigated. The lengths of 2-12 years old herring (present in the catches of both periods) that were only caught with 26 mm mesh size were compared between the two sampling periods. There was still a marked difference in length (1960s: mean 25.9 cm  $\pm$ 2.2, 2000s: 30.9 cm  $\pm$ 2.6 ( $p < 0.001$ )). The increased size in the 2000s was thus not due to net selectivity.

Figure 5 gives the general relationship between VS and age and indicates that VS of two years old herring that were only caught in the 1960s and 2000s were markedly higher ( $> 57.0$ ) than for other age groups. VS of 3-4 years old herring also tended to be higher. For older herring (5-11 years old), VS was relatively low (mean VS about 56.6).

To investigate whether there was any difference in VS between fast and slow growing individuals indicating different origin, VS was compared between fish with length-at-age closest to the VBGF of the 1950s and the 2000s, respectively. Figure 6 shows that young herring (3-4 years old) with length-at-age closest to the VBGF of the 2000s (see Figure 3, green curve) had higher VS in the 1950s, 1960s and the 2000 YCs than specimens of the same YCs with length-at-age closest to the VBGF of the 1950s (red curve in Figure 3). This indicates that these two groups of young herring belong to different components. For young herring of the 1970 YCs, on the other hand, VS of the rapid and slow growing components were overlapping. For the older fish (5-11 years old) VS was in general similar to VS of the slow growing young herring (about 56.6, Figure 6). In the 1950 YCs there were a few fast growing high VS individuals also among the older herring, which indicates that also this component to some extent was present in Lindåspollene among herring more than 4 years old (see also Figure 3). VS for slow growing old age groups of the 1990s and 2000s were lower (56.4) than for the other groups. For both young and old herring, fewer fish were associated with the rapid growing curve in the 1950s than in the 2000s.

### **Overlap in spawning time between the components**

A prerequisite for the existence of a metapopulation is that there is an overlap in timing of spawning between the components. To investigate the spawning overlap between slow and rapid growers, the maturity states of young ( $< 5$  years old) and older (5-11 years old) herring were compared in the 1960s (P1), 1970-80s (P2) and the 2000s (P3, Figure 7). In both March

and April, young and old herring of both growth groups had similar maturity states in all periods. This strongly supports that the time of spawning of the components overlapped.

A more detailed analysis was made on data collected in November 1963 to April 1964 when herring were sampled throughout the maturation period. Figure 8 shows that the herring of YCs 1959-1961 had similar maturation patterns, and a large majority of the herring from all YCs was in stage 6 ('spawning') or 7 ('spent') in April. There was no decreasing trend in length during the maturation period (Figure 8), which would be expected if the fast growing component left before spawning. On the other hand, the 1959 YC despite being the oldest had generally smaller length and lower VS than the other YCs supporting that fast growing herring disappear from the area at a certain age (Figure 8).

## **DISCUSSION**

We have found evidence that different components of Atlantic herring occur together in a semi-enclosed system. The degree of presence of the different components changed throughout a 50 year time period, which for the first time documents a long-term highly dynamic relationship between population subunits in a pelagic fish species during reproduction. The subunits presumably spawn together, and an increased connectivity changed over time several life history traits in the initially slow growing and short-lived component.

The long period with data collection allowed us to track changes over time and reveal new aspects of the dynamics of the population structure of herring, even though variations in sampling effort limited the temporal resolution of the dynamics. Different components could be distinguished based on the growth patterns in combination with VS. Environmentally modulated meristic or morphometric features like VS and otolith microchemistry [48] are often better for characterizing herring populations than standard genetic techniques [49]. VS in herring are primarily determined by the environmental conditions during the embryonic stages [45], [50], [51] and have thus the potential to distinguish components with different distribution and migration patterns.

### **The components of herring in Lindåspollene**

During sampling period 1 in the 1960s, two modes could be distinguished in herring up to 4 years with one component consisting of slow growing herring with low VS and the other

component of fast growing herring with higher VS (Figures 3 and 6). Slow growth and low VS characterize local herring populations along the Norwegian coast [22], [25], and the first component was therefore interpreted as local Lindås herring. Rapid growth and high VS characterize NSS herring [18], and it is well documented that NSS larvae may hatch offshore and drift into the fjords (e.g., [32], [33]), so the second component was interpreted as oceanic NSS herring. Almost all older fish belonged to the first category.

During sampling period 2 in the 1970-80s, both young and old herring of the fast growing as well as slow growing component had low VS. The population of NSS herring had then collapsed, and the remaining herring stayed at the Norwegian coast throughout the year [31], [52], [53]. Spawning occurred more inshore than the traditional spawning sites on the large banks, with the vast majority of the progeny in coastal nursery areas instead of in the Barents Sea [32]. In our samples a component with large size like oceanic NSS herring but with low VS as the local herring could be identified, in particular among young herring (Figures 3 and 6). The similar VS suggest that the NSS herring growing up at the coast mix with and utilised similar spawning areas as local populations [54]. We thus interpret this component as coastal NSS herring. The slow-growing component was interpreted as local herring as in period 1.

During sampling period 3 in the 2000s, when the population of NSS herring had recovered, VS again increased in fast growing young fish (Figure 6). Hence, the decrease and subsequent increase in VS in young fish is in accordance with the decline and rise of the oceanic population of NSS herring. In older fish VS were generally low supporting that relatively few old oceanic NSS herring were present. Interestingly, the slow-growing component with low VS had now more or less disappeared and been replaced by a fast-growing component with low VS interpreted as local fast-growing herring. The main increase in length-at-age took place from the 1970s to the 1990s YCs. Most herring in Lindåspollene in sampling period 3 were thus presumably fast growing local herring and oceanic NSS herring, but a few slow-growing local fish still seemed to be present (Figures 3 and 6). Any remaining coastal NSS herring could not be distinguished from fast growing local herring.

### **Genetic exchange between the subunits**

So do NSS herring actually spawn with local herring? Young NSS herring stayed together with local herring in Lindåspollene in the spawning season, and based on the occurrence of maturation stages, slow growing and fast growing individuals had synchronized maturation,

also when gonad maturity stages reached 6 ('spawning') and 7 ('spent'). In addition, the consistency in length throughout the maturation period in 1964 indicates that the larger NSS herring stay in Lindåspollene throughout the spawning. The available evidence thus supports that local herring and NSS herring interbreed in Lindåspollene. The observed changes in life history traits in local herring provide further support for this.

### **Interplay between genetic and cultural factors**

Migration patterns in herring are presumably maintained by local traditions [55]-[58], and pre-spawning herring in Lindåspollene have aggregated in a restricted area for several decades [20], [59], [60]. When different subunits of herring come into contact there is not only a potential for genetic exchange, but also a possibility that the behaviour is influenced by social transmission. If the NSS herring first time spawners from fjord nurseries encounter schools of local fish, they may join the school during the first spawning. Likewise, NSS herring may have initiated a change in migration strategy (see also [61]) of local herring to travel to more productive outside waters resulting in increased growth and condition over time. Generally poor oxygen conditions in Lindåspollene result in low zooplankton biomass compared to the outside Lurefjord [41], [62]-[64] and a dominance of small copepods [42]. In addition, as there is a genetic basis for migratory behaviour [65], [66] interbreeding with migratory NSS herring may have strengthened the migration tendency in local herring. There are few data on movements in and out of Lindåspollene (but see [40]), but local herring could in this way have realized their genetically increased growth potential. It is thus reasonable to assume that there is interplay between genetic factors influencing both the growth potential and migratory tendency and a change in migration traditions.

### **Changes in life history traits and the fate of Lindås herring**

The mean age and weight of the herring in Lindåspollene increased by almost 100 % from the 1960s to the 2000s. At the same time age at maturity remained stable, whereas the length at maturity decreased from the 1960s to the 1970-80s and increased again to the highest level of the time series in 2000s. It is likely that the length at maturity of the local component in fact remained stable from the 1960s to the 1970-80, whereas the increase until 2000s was representative of a real change in the population. The observed difference in length at maturity between 1960s and 1970-80s was probably a result of two factors: Firstly, there was a strong appearance of NSS herring YCs (1960-62) with high length at maturity [67] in the 1960s. Secondly, there was a skewed sampling from all seasons in the 1960s towards mainly

autumn sampling in the 1970-80s, implying that herring in the 1970-80s on average were caught later in the maturation phase than in the 1960s, i.e. herring not mature in spring, could start maturing during autumn. The marked changes in age, size and length at maturity observed over the time series could be a consequence of phenotypic plasticity, genetic responses or a combination of the two [68]. Herring is a flexible species, and a high level of adaptability is a basic trait of this species [69]. The genetic structure of life history traits and a high genetic diversity may provide a flexible species with large phenotypic plasticity and/or a large potential for rapid evolutionary changes [70], [71]. Rapidly fluctuating environments may favor flexibility and plasticity, whereas longer fluctuations may favour the evolution of enhanced evolvability [71].

With regard to phenotypic plasticity we have no indications that the environment in Lindåspollene has improved for herring. In spite of large annual variations there are no trends in temperature, and the data, though sparse, on the abundance of the main prey of herring *C. finmarchicus* [72], [73] in fact indicate a decrease (unpublished data). The alternative, that herring migrate out of Lindåspollene to more favourable feeding areas resulting in faster growth, is thus more likely. These migrations may have been triggered by NSS herring. It is not obvious how a plastic response to changes in food could explain the increase in age, but faster growth in combination with a size-dependent mortality [74] may to some extent influence longevity.

Another explanation, complementary to the previous, is that interbreeding with NSS herring has changed genetically determined life-history traits from slow growth and short life span [22], [25] to faster growth and longer life [31]. Fish have limited energetic resources and there are trade-offs between somatic growth, survival and reproduction [75], [76]. The heritability of life history traits is quite large [77], and the traits are under selection to maximize fitness. Individuals of the freshwater fish vendace (*Coregonus albula*) colonizing a new habitat respond within a few generations with a change in multiple life history traits with large size and low mortality replaced by small size, high mortality and earlier reproduction [68]. Rapid growth should be crucial for the highly migrating NSS herring as energy costs for swimming decrease with increasing size [56]. Lindås herring is, on the other hand, believed to be relatively stationary, and large size is then less critical. Allocation of resources into high fecundity is traded off against somatic growth and survival [78], and the trade-off between growth and reproduction is generally strong in herring [79], [80]. Lindås herring should thus

be expected to invest strongly in reproduction, and the reproductive effort (RE) in the 2000s was in fact considerably higher than that of NSS herring [27], and unpublished observations from the 1970s indicate a similar RE. A high investment into reproduction can only be achieved by taking higher risks [81], which could explain the initial short life span of Lindås herring. Hence, whereas the growth rate and life span in Lindås herring became similar to that of NSS herring in the 2000s, RE was still high. What is genetically determined is not a set value but a reaction norm [67]. By short migrations to outside productive waters Lindås herring could obtain more resources with low energy costs and thereby combine rapid growth and longevity with high RE.

### **Conclusions and perspectives**

The present study spans over a long time period but is very restricted in the spatial dimension. Resolving the interactions between subunits of a pelagic species with large scale migrations at a given point in space may in fact allow a better resolution of the dynamics compared to open ocean studies involving complicated interactions between the spatial and temporal dynamics. We have provided new evidence that Atlantic herring form a metapopulation and for the first time demonstrated strong dynamics between the subunits over an extended period of time during reproduction. When NSS herring after the collapse underwent a distributional shift (a breakpoint, see [82]), the connectivity with local herring increased and thereby changed life history traits of the indigenous herring by interbreeding and/or a culturally mediated migratory shift.

Even though the data material is unique and our explanations are plausible, we acknowledge that some questions still remain unanswered. Most importantly, the dynamics of the NSS herring in Lindåspollene is not well understood. We know from the growth pattern that most NSS herring migrate out after a certain age, but whether they also migrate in and out before reaching this age is not known. If they migrate in and out this could explain the faster growth of NSS herring. If not, the fast growth is genetically determined. This dynamic of NSS is crucial also for understanding the dynamics of the local herring in periods of high connectivity.

Lindåspollene is geographically positioned closer to the migration routes of NSS herring than other local populations along the Norwegian coast where similar changes in life history traits are not observed, such as Trondheimsfjorden [26] and Lusterfjorden [19]. Historical records



indicate that NSS herring have undergone large fluctuations during the last 500 years ([83] and references therein) causing changes in migration routes [31]. Hence, the original differences between Lindås and NSS herring followed by the later increased inflow of NSS herring could suggest a cyclical pattern with periods of weak connectivity interspersed by periods of strong connectivity. In periods with restricted gene flow there could be a genetic differentiation of the local population resulting in slower growth and shorter life span. After periods with genetic exchange breaking down the genetic differences only herring staying inside or around Lindåspollene will sustain the local population. The basis for maintaining the identity of the local population could thus be a culturally mediated migration pattern. McQuinn [15] argued that the structure of herring populations is of a behavioral rather than genetic nature, and a metapopulation of herring and other species could thus consist of subunits having variable genetic differences but with a cultural diversity as an additional isolating mechanism.

Our study suggests that anthropogenic influence like fishery should not be considered in isolation for a local population. Exploitation of neighbouring subunits alters the composition of the metapopulation that could challenge the integrity of the local population. High rates of connectivity between subunits may decrease productivity and stability of the population [84]. Further studies on the dynamic interchange between different components in marine species and the relative importance of genetic and cultural factors behind the subunit structure are warranted both from a basic ecological and evolutionary perspective and as a basis for sound management.

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Table 1. Summary information of herring samples from Lindåspollene 1962-2011, with sampling month, total number of fish analysed (Total n), number of gillnet settings\* (n settings; prior to 2008 number of settings given as series of gillnets), number of fish sampled for age determination (Age) and VS.

Year	Month	Total n	n settings	Age	VS
1962	11	350	3	304	346
1963	3, 9-12	425	8	402	410
1964	1-7	809	14	747	478
1970	10-11	129	3	125	128
1971	1-11	978	13	925	566
1972	1,3-5, 8, 10-11	569	8	526	146
1973	1-3, 7, 9-10	266	8	258	50
1974	1-4	405	7	396	-
1975	3, 4	150	2	147	-
1977	3, 4, 9	751	9	652	-
1978	3, 4	340	7	331	-
1979	4, 9, 12	309	4	294	-
1980	3-5, 9-11	554	8	464	231
1981	3, 9	356	4	351	251
1982	1, 3	331	3	324	324
2005	2, 9	292	3	284	180
2006	2, 3, 10	351	4	325	89
2007	1-4	336	14	329	329
2008*	1-4, 10-11	749	60	729	10
2009*	1-4, 9	1035	75	875	92
2010*	2-4, 8-10	1564	72	673	668
2011*	4, 9	910	21	870	846

Table 2. Age, length, weight and condition factor of herring ( $\geq 2$  year old) in the different sampling periods. Values are given as mean  $\pm$  SD (min-max). n indicates the number of fish sampled for in the different parameters.

Parameters	P1 (1960s)	P2 (1970-80s)	P3 (2000s)
Age	4.4 $\pm$ 1.7 (2-13)	5.4 $\pm$ 2.3 (2-15)	8.4 $\pm$ 4.2 (2-20)
n (Age)	1453	4789	4137
Length (cm)	25.9 $\pm$ 2.2 (19.5-33.5)	27.2 $\pm$ 2.7 (17.5-35.0)	31.3 $\pm$ 2.4 (22.0-44.7)
n (Length)	1584	5059	5152
Weight (g)	134 $\pm$ 37 (55-275)	166 $\pm$ 53 (35-415)	256 $\pm$ 62 (81-602)
n (Weight)	1579	4797	5119
Condition factor	0.75 $\pm$ 0.09 (0.51-1.22)	0.79 $\pm$ 0.10 (0.35-1.23)	0.82 $\pm$ 0.11 (0.28-1.22)

## Figures

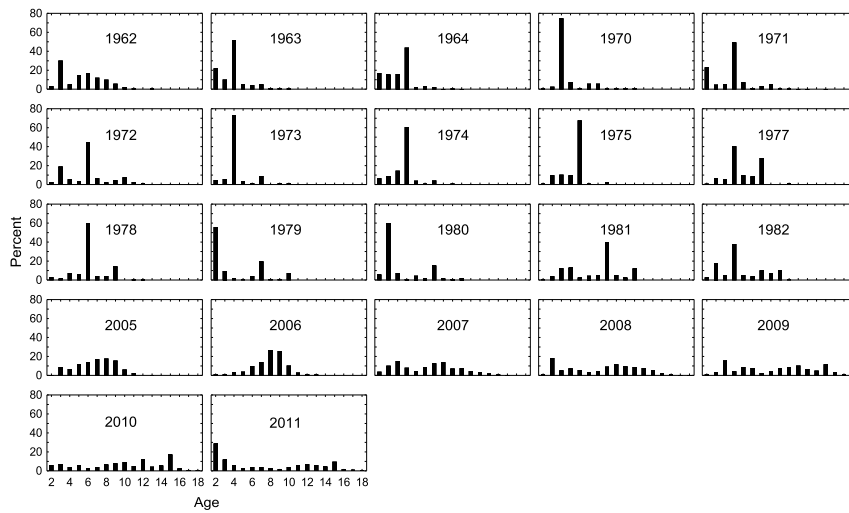
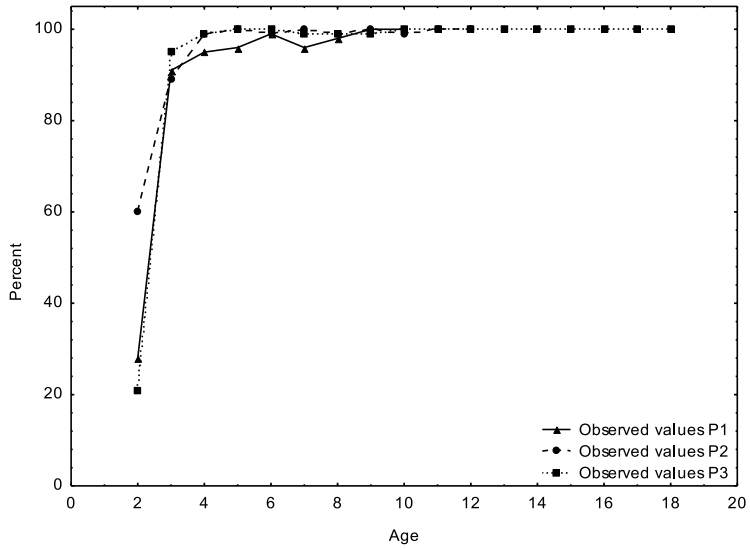


Figure 1. Annual age distribution (% by number in catches) of all herring sampled (1962-2011).

a)



b)

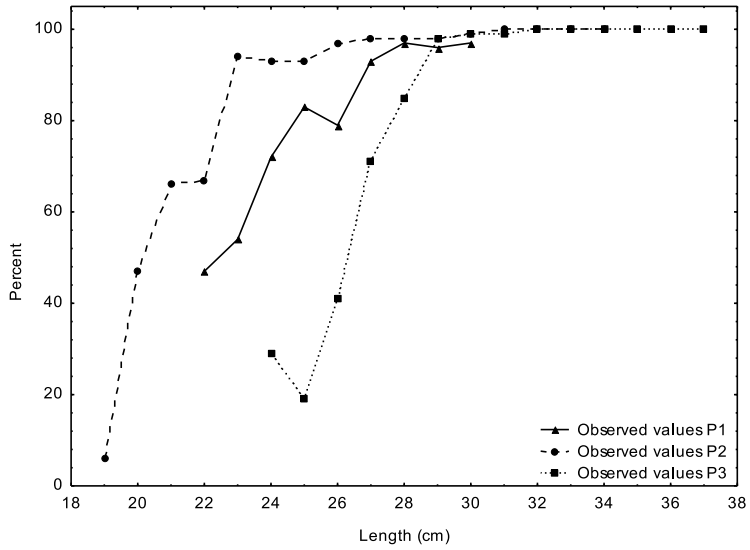


Figure 2. Maturity oogives showing proportion (%) in maturity stages 3-8 at (a) age for the periods P1, P2 and P3, and (b) length for the same three periods.

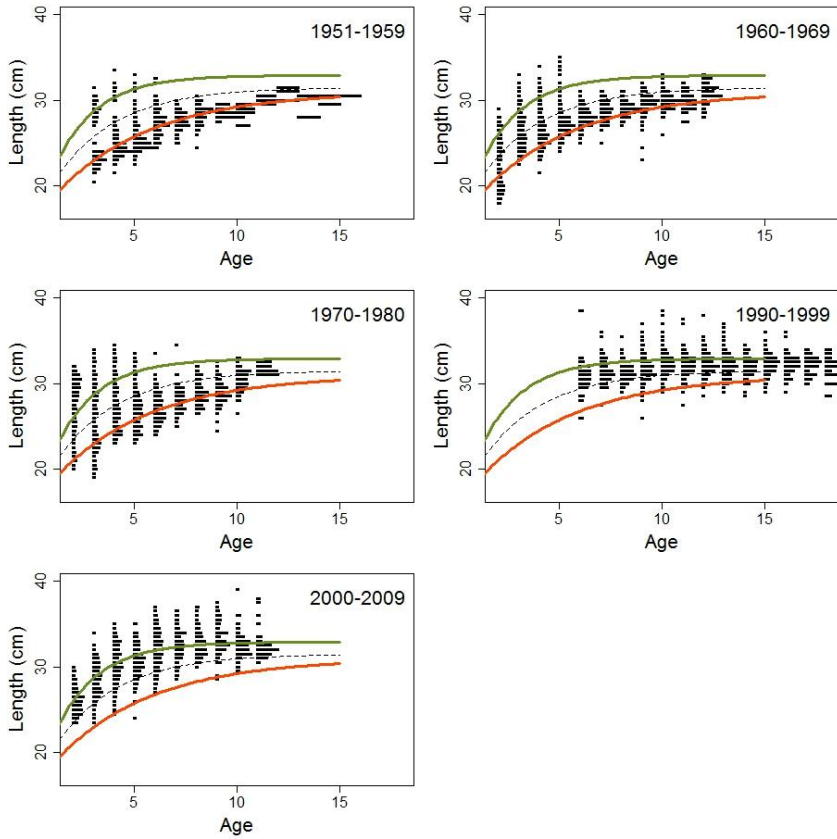


Figure 3. Length at age histograms averaged for YCs of the 1950s, 1960s, 1970s, 1990s and 2000s. A von Bertalanffy growth curve is fitted for the 1950s (red) and for the 2000s (green) and the dotted curve marks the midpoint between the two fitted curves.

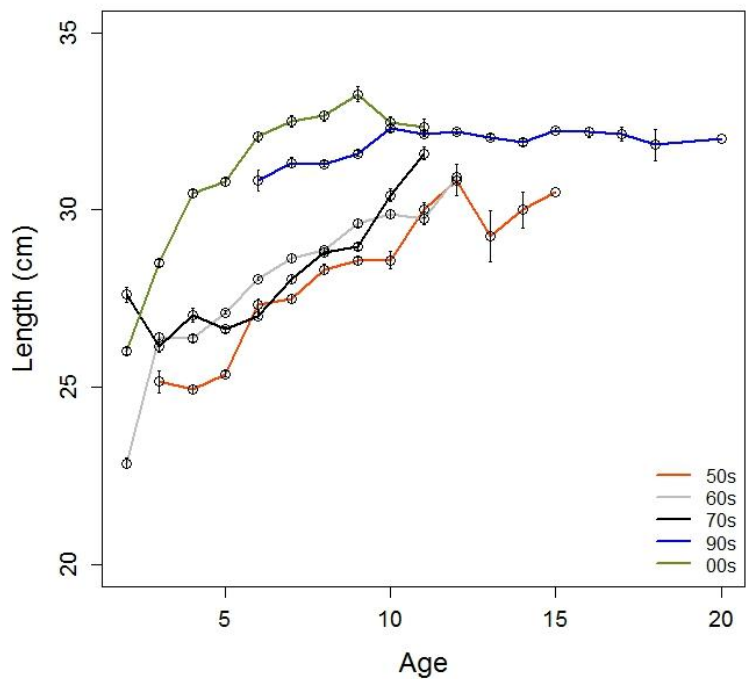


Figure 4. Average length at age  $\pm$  SE of YCs of the decades 1950s to 2000s.

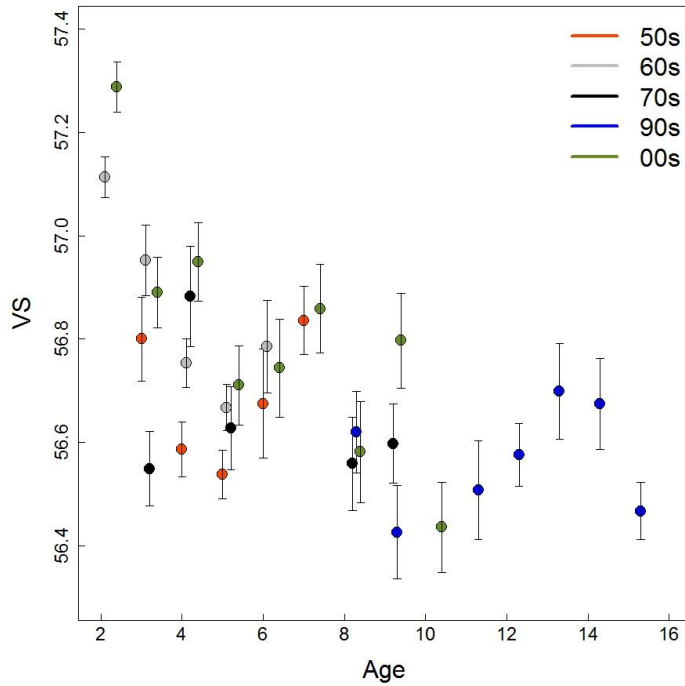


Figure 5. Mean VS ( $\pm$  SE) per age group and decade. Sample sizes  $< 50$  are excluded.

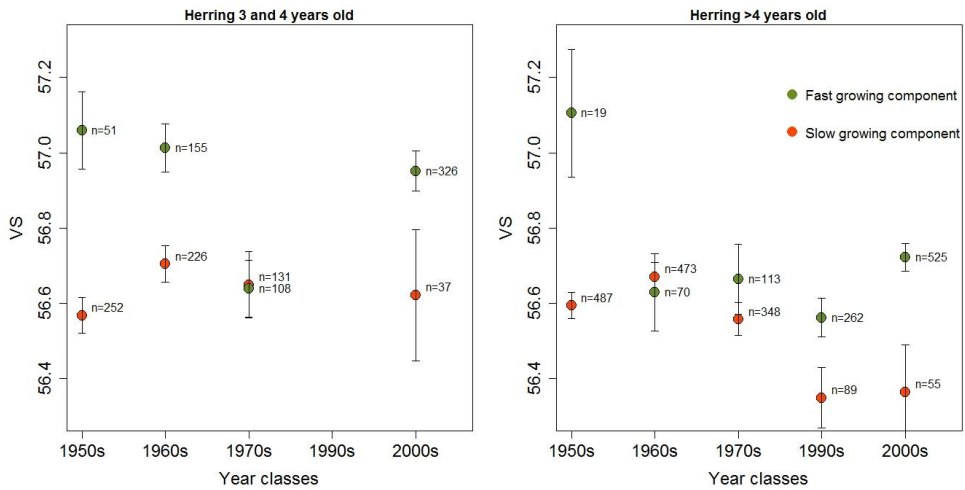


Figure 6. Mean VS ( $\pm$  SE) per decade for young ( $\leq 4$  years old, left) and older fish (right). Individuals with length at age closest to the 1950s slow growing curve shown in red and the ones closest to the 2000s fast growing curve shown in green. Sample size is given for the different components.

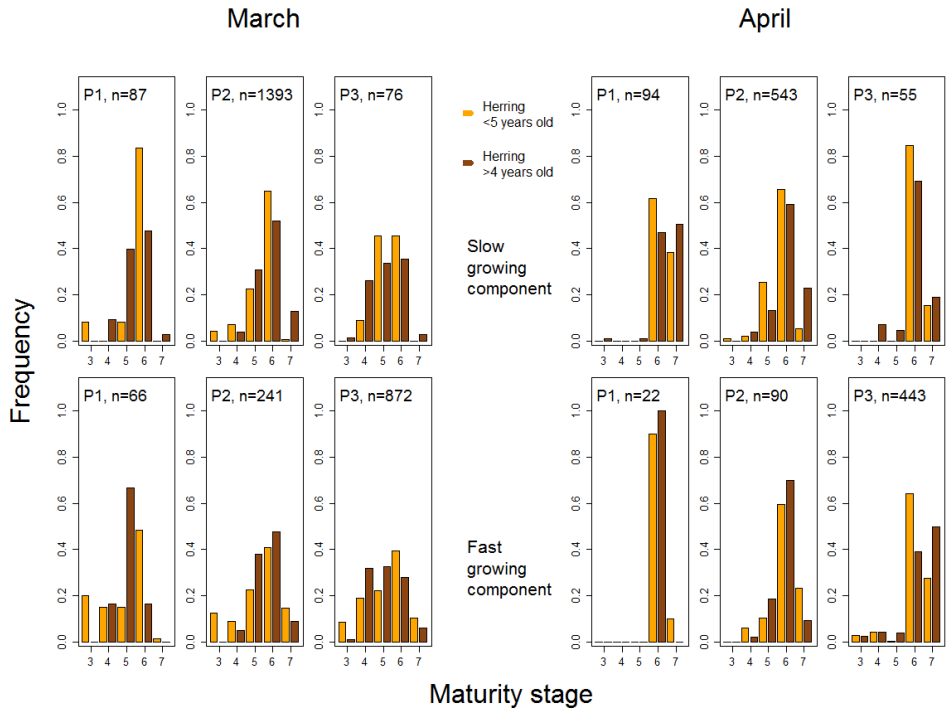


Figure 7. Maturity states of herring in March and April in P1, P2 and P3 for the slow growing (upper panels) and fast growing (lower panels) components of young (orange) and older (brown) fish.

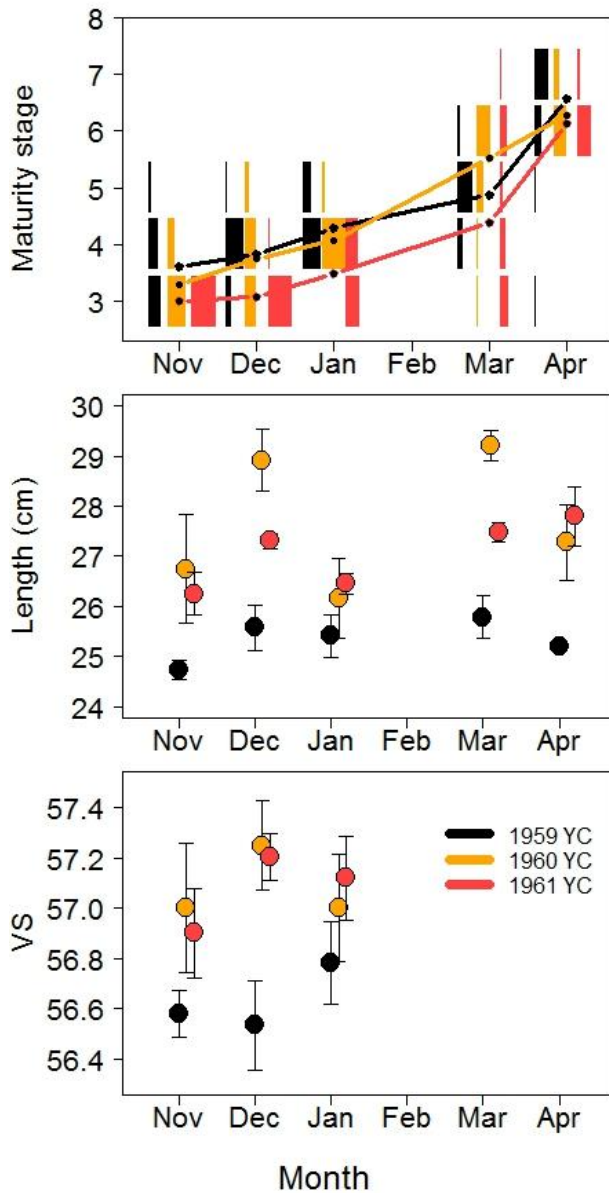


Figure 8. Monthly mean values of maturity stage, length and VS of herring in the period November 1963 through April 1964. Relative monthly proportions of maturity stages are given for each of the 1959-61 YCs.





Illustration: Åse Husebø

# 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<sup>2</sup>) 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 pallasii* (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 & Taggart 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

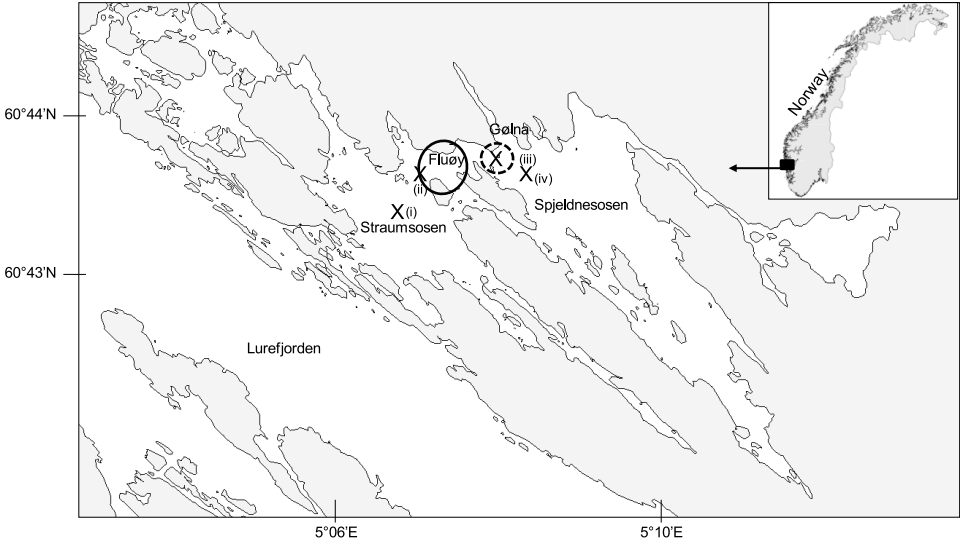


FIG. 1. Map of Lindåspollene, where X denotes the positions for the CTD stations, open circle denotes the main spawning grounds (2006-2010) and the dotted open circle indicates the overwintering area.

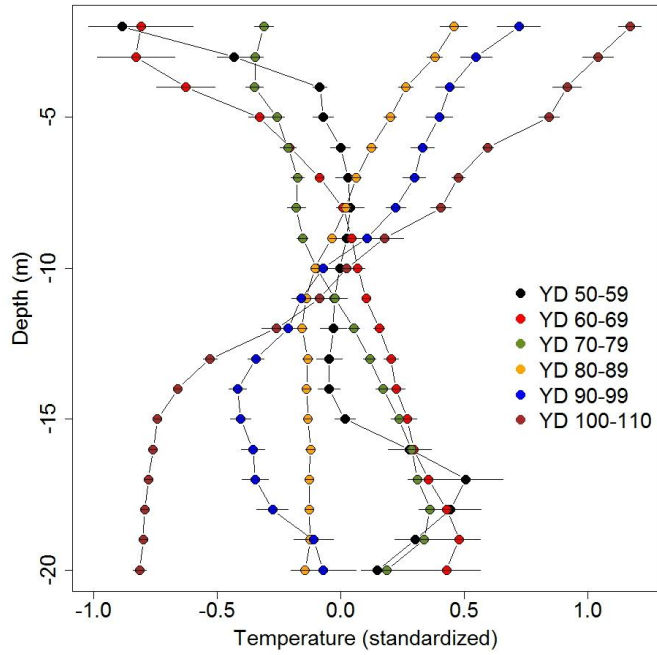


FIG. 2. Standardised temperature at depth averaged over 10 days over all stations and years (mean $\pm$ SE).

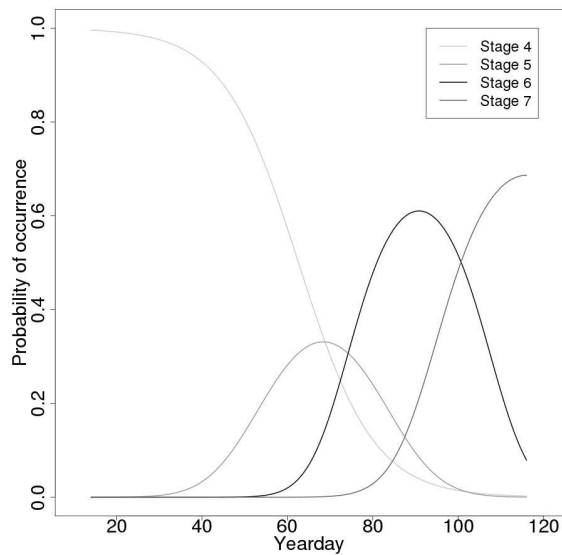


FIG. 3. Maturation model - The lines show the probabilities of finding a given maturation stage of herring depending on yearday (see methods for further details of the model).

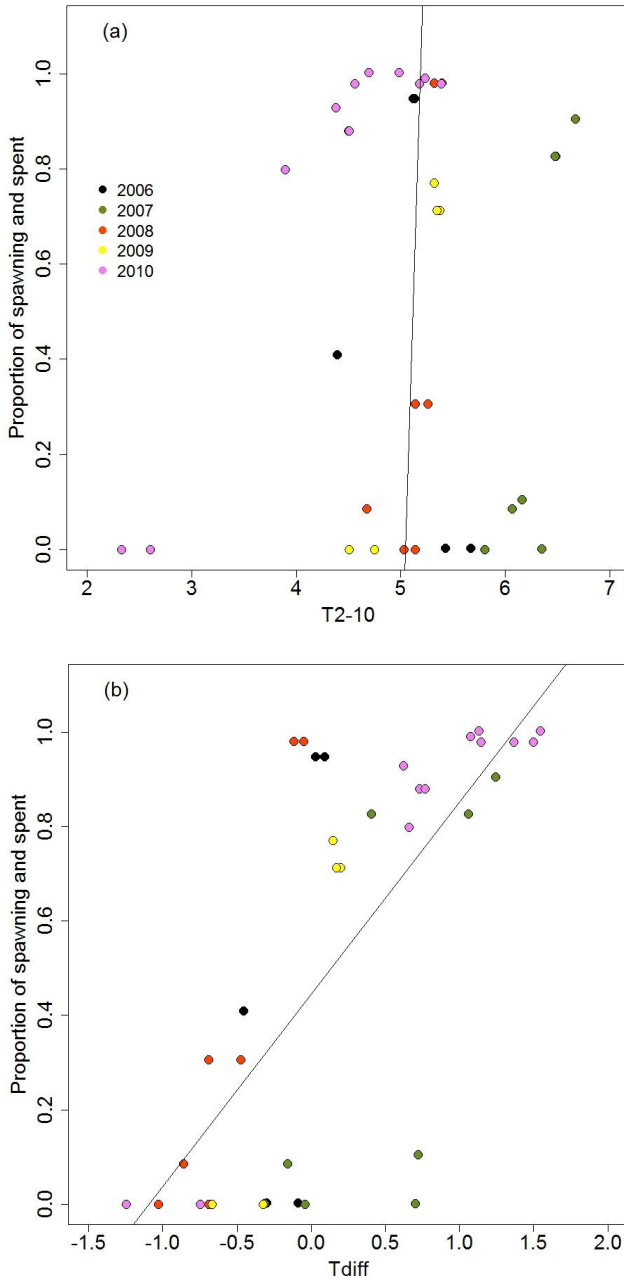


FIG. 4. Proportion of herring in spawning or spent stage (GMI 6-8) as function of (a) mean temperature in the upper depth stratum (2-10 m; T2-10) and (b) mean difference between temperature in the upper (2-10 m) and lower (10-20 m) depth strata (Tdiff). Solid lines indicate the fits from linear regression models.





Same procedure as last year, Miss Sophie?

Same procedure as every year, James!

Illustration: Åse Husebø



# **State-dependent spatial and intra-school dynamics in pre-spawning herring (*Clupea harengus* L.): site fidelity within a semi-enclosed coastal marine ecosystem**

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## **ABSTRACT**

Distribution and aggregation patterns of pelagic fish in marine ecosystems are hard to predict and understand, particularly since focused studies are typically limited to single field efforts. Our study targets coastal pre-spawning herring in a small semi-enclosed coastal marine ecosystem, investigating their spatial and intra-school dynamic characteristics during the pre-spawning period over 6 consecutive years by means of hydro-acoustic surveying. Prior to spawning the herring were consistently located at a specific site characterised by a deep trench that led to the deepest basin in the system and provided a potential escape route from predators. As the herring approached spawning, they moved in the direction of the spawning grounds, mimicking the long-distance spawning migration of Norwegian spring spawning herring. There were consistent trends across years in the school characteristics demonstrating state-dependent schooling dynamics. Schools were found closer to the bottom and more densely packed during late than early pre-spawning. Furthermore, a higher diversity in maturity stage between individual herring, assumed to be associated with stronger motivational conflicts, resulted in increased heterogeneity in school packing density. Our repeated investigations from a small site pinpoint some key behavioural traits in herring trading off survival, energy saving and reproductive success.

**KEY WORDS:** Herring · Spawning · Spatial dynamics · School dynamics · Gonad maturity state · Hydro-acoustics

## INTRODUCTION

Pelagic schooling fish are abundant and play a key role in most marine ecosystems (Pikitch et al. 2012). Their spatial distribution is determined by a complex set of motivational and environmental factors (Krebs & Davies 1978) that makes it hard to predict (Pitcher & Parrish 1993). Since schooling dynamics are the collective output of behavioural decisions, the spatial positioning at any point in time is the result of individuals compromising stimuli from their environment, their neighbouring conspecifics and their internal motivational states, such as hunger and fear (Pitcher & Parrish 1993, Parrish & Edelman-Keshet 1999). In spite of the complex nature of schooling, field studies of schooling dynamics are typically limited to single efforts, either recording multiple schools over large areas or by monitoring single schools over a restricted period of time. Based on such efforts plausible adaptive explanations for observed aggregation patterns and behaviour may be put forward, but alternative explanations can usually not be properly assessed, and the biological states of the fish are rarely taken into account (but see Nøttestad et al. 1996, Mackinson 1999, Axelsen et al. 2000).

Herring spend most of their life in schools (Blaxter & Hunter 1982, Fuiman 1989), but schooling dynamics change as they go through different life history and seasonal phases. In the spawning period, the morphological and structural features of herring schools change markedly over time (Nøttestad et al. 1996, Axelsen et al. 2000). The suggested explanation is that differences and changes in individual motivational state affect intra-school dynamics. Axelsen et al. (2000) observed a single spawning herring school split partially into one pelagic and one demersal component and attributed this to motivational conflicts between pelagic pre- and post-spawners avoiding the risky demersal zone and ripe herring searching towards the bottom to spawn. Such state-induced intra-school dynamics in herring have later been verified both in field studies (Johnsen & Skaret 2008) and through modelling (Vabø & Skaret 2008).

The schooling dynamics of herring in the pre-spawning period have been less studied. Norwegian spring spawning (NSS) herring populations typically overwinter in immense schools before undertaking long migrations to coastal spawning areas in January or February (Kvamme et al. 2003, Holst et al. 2004). During overwintering, feeding ceases and gonads build up, while predator avoidance and energy conservation are given priority (Huse & Ona

1996, Slotte 1999). In smaller, local herring populations the dynamics are different, with shorter distances between pre-spawning and spawning areas and fewer individuals to join for protection (Fernö et al. 1998). How this influences the schooling dynamics is still unknown.

The semi-enclosed fjord system of Lindåspollene in south-western Norway is inhabited by a small herring population, the Lindås herring, whose presence has been documented regularly since 1962 (Anon 1969). The herring in this ecosystem has been observed to aggregate in a single large school before spawning (Lie et al. 1978, Aksland 1983), but whether this is a consistent feature of the local population over time has not yet been determined. The main objectives of this study were to establish whether the local herring consistently aggregate in this manner during the pre-spawning period and to quantify the school dynamic features in relation to the development and variability of gonad maturity state. Two specific questions were addressed: (i) Does gonad maturity influence schooling dynamics? and (ii) Does variability in gonad maturity between individuals affect schooling dynamics?

## **MATERIALS AND METHODS**

Lindåspollene is a small semi-enclosed coastal marine ecosystem near Bergen in south-western Norway (Fig. 1a). A narrow sill (7.5 m wide, 3.5 m deep) connects the adjacent fjord (Lurefjorden) to Lindåspollene, which consists of 3 distinct, 60 to 90 m deep basins. Between the outer basin Straumsosen (maximum depth: 60 m) and the middle and deepest basin Spjeldnesosen (90 m), there is a 5 to 10 m deep sill (Aure 1972). The inner basin Fjellangervågen (75 m) is anoxic from a depth of ~18 m to the bottom (Dahl et al. 1973), and adult herring have rarely been observed there (pers. comm. R. Bergfjord). A general description of the Lindåspollene ecosystem (topography, hydrography, biota features) can be found in Dahl et al. (1973) and in Dahl & Lie (1981). The relatively sheltered Lindåspollene differs from Lurefjorden with regard to environmental conditions, species abundance, and food organisms (Dahl et al. 1973, Lie et al. 1978). Lindåspollene is characterized by moderate boat traffic, and only small-scale gillnet and hand line fishing is permitted, making it ideal for small-scale ecosystem studies. During the winter, Lindåspollene is often ice-covered (Wassmann 1983), which puts constraints on fieldwork. The Lindås herring is a key species in this ecosystem (Lie et al. 1978, Langård et al. 2006), and has been described in detail by Lie et al. (1978).

## **Survey design**

In order to locate the herring in the pre-spawning period, acoustic surveys (Fig. 1a, modified according to ice cover) were performed by the research vessel RV ‘Hans Brattstrøm’ (24.3 m LOA, 6.5 m width, 79 GRT) between February and April from 2006 to 2011. The availability of the vessel placed some constraints on the timing and duration of each monitoring period. All surveys were carried out in daytime. Each survey period started with a 7 hour-long meso-scale survey at 3-5 knots (08:00-18:00 h local time), covering the most of Lindåspollene, followed by high-density mini-surveys in areas where herring had been observed (Fig. 1a). The mini-surveys were carried out at relatively slow speeds (2-3 knots), with transect line spacings of 5-15 m. The repeated short and close transect lines involves a certain risk of pseudoreplication, but the studied schooling behaviour may potentially change within seconds, and overall the samples covered different time periods (Fig. 2a) with data from several years.

## **Data collection**

### *Acoustic recording*

Acoustic data were recorded using a Simrad EK60 split-beam echosounder operating at 38 kHz. The transducer was mounted on the hull of RV ‘Hans Brattstrøm’ 1.2 m below the surface. This vessel has previously been shown to have negligible impact on herring behaviour (Axelsen et al. 2000, Skaret et al. 2005). In 2010, the observations were supplemented by data collected in February and March using a small boat (15 ft Pioneer) equipped with a 15 HP engine, running a Simrad EK60 split-beam echosounder operating at 120 kHz. The transducer was mounted at the bow of the boat and submerged to about 0.25 m below the surface during operations. Transmission power of 1000 W was used for both echosounder systems, while pulse durations of 1.024 and 0.256 ms were used for the RV ‘Hans Brattstrøm’ and the Pioneer, respectively. In 2008 a stationary acoustic underwater platform with a Simrad EK60 120 kHz split-beam echosounder (Svelling et al. 2002, Langård et al. 2008) was used in order to monitor diel variations in schooling. A total of 172 school observations were made during the 6 years of the study.

### *Biological sampling*

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. These mesh sizes were chosen in order to fish selectively for herring larger than 20 cm total length, while allowing juveniles to pass through. The gillnets were set in 3 series of 3 nets each near the surface (max depth 5 m). We may ask whether the herring sampled in the upper 5 m are representative of the acoustic observations, but the recordings from the stationary acoustic platform showed that the school dissolved into surface layers at dusk, which is typical for herring in this period (Blaxter 1985, Skaret 2007). The gillnets were positioned so as not to interfere with boat traffic but as close to the pre-spawning area as possible, and always within a 450 m radius (Fig. 1b). Additional monofilament gillnets and entangling nets (57-79 mm mesh sizes) were set on the bottom in order to catch potential predators on herring and herring eggs such as cod (*Gadus morhua*), pollack (*Pollachius pollachius*) and haddock (*Melanogrammus aeglefinus*), and to monitor the presence of herring eggs in their stomachs, serving as indications of the time of spawning. Nets were set in the afternoon (between 17:00 and 19:00) and hauled the next morning (09:00-12:00).

Individual herring were measured for total length (L) to the nearest 0.5 cm below and total body weight (W) to the nearest g below, and 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). Herring stomach fullness was estimated in 2008 to 2011 according to a relative 6-point scale on which 1 corresponded to empty stomach and 6 to full (Mjanger et al. 2011).

Fulton's condition factor K (Ricker 1975) was calculated for all sampled herring as:

$$K = 100 \cdot \frac{W}{L^3} \quad (1)$$

### *Hydrographical data*

Ambient temperature, salinity and oxygen conditions were monitored in the pre-spawning area and at selected sites in Straumsosen and Spjeldnesosen (Fig. 1a) by means of vertical CTD casts using a SAIV model SD204. All CTD casts were deployed from the surface to 5 m above the bottom. Only downcast data were processed.

## Analyses of acoustic data

Volume backscattering strength ( $S_v$ ; dB re  $1\text{m}^{-1}$ ) measurements from the acoustics were analysed using the Sonardata Echoview v.5.1© software. Herring schools were readily identified and distinguished from other acoustic backscatter using a minimum  $S_v$  threshold of -70 db. Measurements of mean school vertical extension (m), mean school depth (D; m) and distance from the bottom to the deepest extent of the school (m) were recorded. The herring packing density  $\rho$  ( $\text{m}^{-3}$ ) was estimated according to:

$$\rho = 10^{\left(\frac{S_v - TS}{10}\right)} \quad (2)$$

and

$$TS = 10 \cdot \text{LOG}_{10}(\sigma_{bs}) \quad (3)$$

where  $\sigma_{bs}$  is the backscattering cross section ( $\text{m}^2$ ) of the acoustic target,  $S_v$  is the mean school volume backscattering strength (dB re  $1\text{m}^{-1}$ ) and TS is the Target Strength (dB re  $1\text{m}^2$ ) (MacLennan et al. 2002). The following relationship between TS, L and D was used (Ona 2003):

$$TS = 20 \cdot \text{LOG}_{10}(L + 0.25) - 2.3 \cdot \text{LOG}_{10}\left(\frac{1 + D}{10}\right) - b_{20} \quad (4)$$

where  $b_{20}$  for herring in February corresponds to -66.1 dB and -68.3 dB for 38 kHz and 120 kHz, respectively (Ona et al. 2001). Note the addition of 0.25 cm to the total length in order to compensate for the practice of rounding down the recorded total length.

The circularity of the school (C) was calculated as:

$$C = \left(\frac{(5 \cdot 10^5) \cdot (P \sqrt{\frac{A}{\pi}})}{A}\right)^{-1} \quad (5)$$

where  $P$  and  $A$  are the estimated vertical cross section perimeter and area of the school, respectively. The heterogeneity in packing density within a school vertical cross section, or the school roughness  $R_{sc}$  (Nero & Magnuson 1989, Gerlotto et al. 1999) normalized to  $\rho$  was calculated as:

$$R_{sc} = \frac{\sqrt{R_h \cdot R_v}}{\rho} \quad (6)$$

where the roughness in the horizontal ( $R_h$ ) and vertical ( $R_v$ ) directions were calculated according to:

$$R_h = \sum \frac{(E_{ij} - E_{i,j+1})^2}{N-1} \quad (7)$$

$$R_v = \sum \frac{(E_{ij} - E_{i+1,j})^2}{N-1} \quad (8)$$

and where E denotes a single sample bin within the school, i is the row (depth) index, j is the column ('ping') index and N is the total number of sample pairs.

In order to assess the possible influence of nearby predators on the recorded school parameters, all single targets in the vicinity of schools were manually identified and classified as potential predators based on echogram appearance. For each school recording, the presence or absence of predators was noted.

### **Location of the spawning grounds**

The location and timing of spawning events were documented whenever possible. In 2006 and in 2008 to 2010 the spawning locations were identified on the basis of video observations of herring spawn and visual observations of large aggregations of common eider ducks (*Somateria mollissima*), which are frequent foragers on herring eggs (Kjørsvik et al. 1990). In these years the spawning grounds were located in the north-western part of Spjeldnesosen, near the shallow threshold separating Straumsosen and Spjeldnesosen (Fig. 1b). The bottom topography at these spawning sites was mostly flat, with a substrate consisting mainly of rocks and boulders. In 2007 and 2011, the locations of the spawning grounds could not be identified.

### **Data analysis**

#### *Maturation model*

The biological dataset for 2006 to 2011 varied with regard to sampling effort between years, depending on vessel availability (Fig. 2a). Statistical modelling was used to calculate the

probability of occurrence of herring maturity stages 4 to 7 by day of the year in order to interpolate the progression of gonad maturity in periods without gillnet samples. The sampling locations are shown in Fig. 2b. We used generalized linear mixed-effects models (GLMMs) with a binomial error term for the calculation of probabilities. The response variable was binary and describes whether a fish was within the given maturation stage or not. A continuous variable that defined the day of the year was the only predictor. In order to allow for a changing slope depending on day of the year, a second order polynomial was included in the model. If non-significant, it was removed from the model. Since samples were acquired over several years, the model took account of random variability due to year.

In order to evaluate whether the individual maturity state of the herring affects schooling dynamics, we defined two categories of maturation: 'early pre-spawning' (probability of Stage 6  $< 0.5$ ) and 'late pre-spawning' (probability of Stage 6  $\geq 0.5$ ). A GLMM with a quasi-poisson error term was used to test for differences between the categories. We used Poisson regression since the variance in the different measures of school dynamics tended to increase with the mean. Depth in the area where each school was recorded was used as a co-variate in the model. The 6 school characteristics (response variables) that were tested in separate models were; 1) Packing density, 2) Vertical extension, 3) Mean depth, 4) Distance from bottom, 5) Circularity, 6) Roughness.

In order to assess whether differences in maturity stages within a school affects its dynamics we followed two main steps. First, we used the probability curves to calculate a Maturity Diversity Index (MDI) that describes the expected diversity of herring maturity within the school depending on day of the year. The MDI values were calculated by using the Shannon Index (Shannon 1948, Simpson 1949) on stage probabilities derived from the maturity stage models. The final MDI measures were rescaled to range only between 0 and 1 (MDI/max MDI). Secondly, the effects of MDI on school dynamics were evaluated through the same type of GLMM as described above for the comparisons between early and late pre-spawning periods. In these models, the MDI values were divided into low and high MDI levels, where the low and high levels are  $< 0.5$  and  $\geq 0.5$ , respectively. The depth in the area where each school was sampled was used as a co-variate in the models.



### *Predation pressure*

The effect of predation presence on school dynamics were analysed using the same GLMMs as described above, but with predation as predictor. This predictor contained the levels “present” or “absent”. All statistics were performed using R version 2.15.2 (R Development Core Team 2012, <http://www.r-project.org>).

## **RESULTS**

With few exceptions, the hydrographic conditions were well within the ranges normally acceptable for herring (Runnström 1941, Fig. 3). Average temperatures were generally between 5 and 7 °C, but 2010 and 2011 were markedly colder than the preceding years. During early pre-spawning in 2010, temperatures were < 3 °C, which is close to temperatures herring tend to avoid (Østvedt 1965). Salinity was generally between 30 to 32 PSU (Fig. 3), albeit somewhat lower close to the surface, probably due to freshwater run-off. Oxygen levels averaged 7 to 8 mg l<sup>-1</sup> but were lower in deep waters early in the study period and were generally lower early in the pre-spawning period in 2009 and 2010 and in the late pre-spawning period of 2007 (Fig. 3). Our data did not permit a formal analysis linking environment and behaviour, but we note that 2009 and 2010 had cold surface waters corresponding with deep school distribution during early pre-spawning (Fig. 3 and Table 1).

In all years our observations suggest that the herring were present in one school. The herring displayed a high degree of fidelity to a small pre-spawning area around Gølna Island. The topography of this area is characterised by a trench that gradually becomes shallower towards the north-west (Figs. 1 and 4). Most schools were observed in the north-western part of the trench, but the herring generally shifted north-westwards towards the shallower spawning grounds during the pre-spawning periods (Linear Mixed Effect; LME ANOVA  $p < 0.001$ ; Fig. 4).

During late pre-spawning, schools stayed closer to the bottom than during early pre-spawning, and school packing densities were also higher (Tables 1 and 2). No differences in the other parameters were found (Table 2).

The Maturity Diversity Index (MDI) reached its maximum prior to the late pre-spawning periods (Fig. 2b). Schools in the high MDI period had higher packing densities, roughness and

circularity, while they remained closer to the bottom than schools in the low MDI period, and the school vertical extension was lower in the high MDI period (Table 2).

The gillnet samples of potential predators confirmed that cod had been feeding on herring (Table 3). Adult consumers of herring were mostly cod > 50 cm in length, while stomachs with content in cod < 50 cm usually contained herring eggs. The vertical school extension unexpectedly increased when predators were present (General Linear Mixed Model; GLMM ANOVA,  $p < 0.05$ ). Other school parameters were not significantly influenced by predator presence.

The lengths and weights of the herring ranged from 305 to 322 mm and from 217 to 293 g respectively (Table 4). The condition factor (K) ranged from 0.75 to 0.88 and was significantly different between years (Linear Model; LM ANOVA,  $p < 0.001$ ). Herring generally had empty stomachs, with only about 3% (stomach fullness 2;  $n = 102$ , 3;  $n = 3$ , 4;  $n = 2$ ) of the fish in the early pre-spawning period and around 11% (stomach fullness 2;  $n = 1$ , 3;  $n = 2$ ) in the late pre-spawning period having any contents.

Anecdotal recordings of predatory seabirds were made. Great cormorants (*Phalacrocorax carbo*) were frequently observed in all years. This opportunistic forager (Steven 1933) can dive to depths of 32 m (Grémillet et al. 1999), but feeds largely on smaller gadoids (Anker-Nilssen & Lorensen 2004). Harbour seals (*Phoca vitulina*), a known predator of herring (Haug 1998), were occasionally observed in 2009 and 2010.

## **DISCUSSION**

To the best of our knowledge this is the first *in situ* study of the dynamics of spatial distribution and schooling behaviour of herring over an extended period of time and in consecutive spawning seasons. Early pre-spawning herring in Lindåspollene consistently displayed fidelity to an area with close access to the deepest basin in the system. As maturation progressed the herring aggregated closer to the spawning ground. When approaching spawning, the schools also remained closer to the bottom, while packing densities increased. The diversity of gonad maturity stages was found to affect the heterogeneity of packing density within the school.

The behaviour of herring during the spawning period can be explained in terms of multiple trade-offs between predation, feeding and spawning (Nøttestad et al. 2004). The herring

displayed low feeding activity. Herring do normally not feed before spawning, but start shortly afterwards (e.g. Parsons & Hodder 1975, Crawford 1980, Huse & Ona 1996, Slotte 1999) reflecting the change in trade-offs between feeding and reproduction (Nøttestad et al. 1996, Axelsen et al. 2000). It is difficult to quantify the effects of predation pressure on school dynamics from our data, even though it was documented that herring encountered various predators, and in some cases had been preyed upon. Herring that aggregate within the same restricted area season after season should be an easy target for predators, and our gillnet samples suggested that herring was a main prey item for large cod. The abundance as well as consumption and digestion rates of cod in the system could, however, could not be quantified.

### **Spatial dynamics and site fidelity**

Pre-spawning herring aggregated in one major school in a small area in all 6 years of our study, confirming previous anecdotal observations (Lie et al. 1978, Aksland 1983). Staying within a limited area could be an energy-saving strategy (see Mackinson 1999), and video observations showed that maturing herring swam slowly around in a circle with extended pectoral and pelvic fins, permitting energy-efficient gliding behaviour while avoiding sinking (see also Huse & Ona 1996, Kaartvedt et al. 2009). The CTD data showed that the hydrography in the pre-spawning area did not differ markedly from the surrounding areas, with similar ranges in temperature and oxygen levels. On the other hand, the pre-spawning area differs in topography and is characterized by a trench that leads directly to the deepest basin (Spjeldnesosen ~90 m). The trench could function as an ‘emergency exit’ for herring under predatory attack. Herring have been reported to hide in deep trenches close to spawning grounds during the day in order to avoid predation (Runde 2005, Skaret 2007), and massive aggregations of overwintering herring in northern Norway stay deep to avoid killer whale attacks (Nøttestad et al. 2002). Herring are specialists in vertical escape (Blaxter 1985), and the fish in Lindåspollene appear to have adopted a precautionary approach by staying in a place that provides an escape route to deeper waters.

As spawning approached, the herring tended to shift their distribution closer to the spawning grounds. Tracking of individual fish in 2010 confirmed this meso-scale movement pattern (Langård et al. unpublished observations). Compared to NSS herring, the potential migration distances of the local herring in Lindåspollene are very short, and the overwintering, migration and pre-spawning periods appear largely to merge. However, the migration patterns in Lindåspollene bear similarities on a small scale to those of NSS herring. The small meso-

scale shift in the distribution of local herring between the early and late pre-spawning period can be seen as a weak reflection of the long-distance migration of NSS herring from their overwintering areas to the spawning grounds. NSS herring have been observed to aggregate close to the spawning area some time before moving on to the spawning grounds (Baker 1978, Aasen 1982, Nøttestad 1994), which could correspond to the observed meso-scale distributional shift in local herring.

### **School dynamic patterns as a function of maturation state**

Herring approaching spawning aggregated in dense schools close to the bottom. Higher packing densities and shorter distances to the bottom closer to spawning have been observed in several studies (Nøttestad et al. 1996, Mackinson 1999, Skaret 2007). High packing density is usually attributed to anti-predator behaviour (Breder 1951), and herring may seek shelter behind conspecifics for protection (Hamilton 1971, Pitcher & Wyche 1983, Pitcher & Parrish 1993, Axelsen et al. 2001). The maturation process could also be accelerated by close contact with ripening individuals releasing pheromones (e.g. Ware & Tanasichuck 1989, Scott et al. 1994, Winters & Wheeler 1996) in a dense school.

A high Maturity Diversity Index (MDI) should reflect high diversity in motivational states among individual fish within a school, which could lead to more variable depth preferences resulting in increased school extension (Axelsen et al. 2000, Skaret 2007, Johnsen & Skaret 2008, Vabø & Skaret 2008). Our results are, however, not in accordance with this, as the vertical extension tended to be low when MDI was high. In the prevailing situation with a relatively small school keeping together for a long time period, herring not ready to spawn may stay close to the bottom together with herring approaching spawning in connection with the collective behaviour of herring (Skaret al. 2003) and thereby not break out in a vertical split. Still, the high heterogeneity in packing density (roughness) associated with high MDI levels may reflect conflicts between individual fish at different stages of maturation.

### **Environment and predation**

Our study design did not permit detailed analyses of links between environmental factors and herring behaviour. However, any variation in temperature, salinity or oxygen levels did not affect the choice of pre-spawning area that remained the same throughout the study period. Our results suggest that environmental conditions to some extent affected school

characteristics, but there were still consistent patterns in schooling dynamics among years that were strongly related to maturation state. As herring would be expected to aggregate more tightly under predatory threat the increased vertical school extension in the presence of predators is difficult to explain, but may reflect vertical avoidance reactions of herring encountering predators.

## **CONCLUSIONS**

Throughout the 6 years of our study, the herring aggregated within a small area for a long period before spawning, confirming that the pattern observed in the 1970s (Lie et al. 1978, Aksland 1983) is consistent. This location may be understood as a ‘base camp’ close to the spawning grounds adjacent to the deepest basin in the system, permitting vertical escape. The preferred conservative strategy of herring (Fernö et al. 1998, Corten 2002, Huse et al. 2010) may well stabilise the choice or pre-spawning area. The meso-scale distributional shift closer to spawning may be analogous to the long-distance migration of NSS herring to the spawning grounds.

The state of maturation influenced several aspects of behaviour. Although the changes were generally relatively small, this demonstrates the need to consider physiological and behavioural states if we wish to understand the dynamics of fish schools. The diversity in maturation states influenced the roughness and vertical extent of the school. Similar indices of variability in maturation state and satiation state (stomach fullness and condition factor) could have a potential in explaining the dynamics of fish schools.

Detailed long-term studies of herring school dynamics in small-scale ecosystems may reveal general state-dependent schooling patterns that are valid also for coastal and oceanic herring populations. Since school dynamics are the output of behavioural decisions in individuals, it is essential to learn more about the behaviour of single fish. Studies of individually tagged herring (Langård et al. unpublished data) could pave the way from state-dependent individual behaviour to a better understanding of dynamics at the school level.

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## Tables

Table 1. *Clupea harengus*. Summary of school descriptor values based on acoustic recordings from 2006 to 2011. ‘Early’ and ‘Late’ refer to early and late pre-spawning periods (see text for details). \* School roughness x 10<sup>3</sup>.

Parameter	Period	Year	Mean	N	SD	Min.	Max.
<b>Packing density (ind/m<sup>3</sup>)</b>	Early	2006	0.95	17	0.94	0.03	2.96
	Early	2007	1.61	39	1.35	0.19	5.87
	Early	2008	0.17	7	0.08	0.08	0.30
	Early	2009	0.88	38	0.96	0.06	4.81
	Early	2010	0.69	12	0.93	0.02	3.37
	Early	2011	0.36	19	0.21	0.01	0.73
	Late	2006	0.35	1	–	0.35	0.35
	Late	2009	2.81	14	4.07	0.11	13.26
	Late	2010	1.63	7	1.22	0.44	4.05
	Late	2011	0.47	18	0.58	0.02	2.55
<b>Vertical extent (m)</b>	Early	2006	6.74	17	2.12	4.32	11.15
	Early	2007	5.35	39	1.65	2.50	10.44
	Early	2008	4.35	7	0.90	2.99	5.48
	Early	2009	8.03	38	3.00	3.18	13.70
	Early	2010	6.28	12	2.80	3.61	12.98
	Early	2011	4.92	19	1.66	2.09	7.89
	Late	2006	8.20	1	–	8.20	8.20
	Late	2009	5.40	14	1.23	3.68	7.56
	Late	2010	5.30	7	1.22	3.41	6.76
	Late	2011	5.04	18	2.02	1.83	8.84
<b>Mean depth (m)</b>	Early	2006	16.59	17	2.16	13.28	21.68
	Early	2007	16.08	39	1.92	10.82	21.16
	Early	2008	15.52	7	2.01	12.95	18.64
	Early	2009	23.37	38	5.13	16.55	36.87
	Early	2010	29.49	12	12.25	16.14	64.20
	Early	2011	18.47	19	3.87	14.35	28.50
	Late	2006	25.45	1	–	25.45	25.45
	Late	2009	21.53	14	4.31	15.83	28.89
	Late	2010	22.47	7	7.07	16.23	33.49
	Late	2011	17.12	18	3.53	5.64	21.13

<b>Distance from bottom (m)</b>	Early	2006	6.78	17	4.44	1.54	16.68
	Early	2007	7.52	39	4.55	0.00	16.09
	Early	2008	8.05	7	2.89	4.16	12.10
	Early	2009	10.73	38	9.69	0.00	39.14
	Early	2010	3.54	12	5.34	0.00	15.30
	Early	2011	9.45	19	4.23	3.28	16.36
	Late	2006	0.64	1	-	0.64	0.64
	Late	2009	2.48	14	3.51	0.00	9.22
	Late	2010	0.00	7	0.00	0.00	0.00
	Late	2011	6.47	18	4.62	2.01	17.66
<b>Circularity (%)</b>	Early	2006	43.96	9	9.29	29.31	54.15
	Early	2007	37.52	39	10.82	18.94	75.59
	Early	2008	12.31	1	-	12.31	12.31
	Early	2009	40.09	8	14.38	27.00	60.61
	Early	2010	38.03	7	9.75	26.99	49.42
	Early	2011	47.83	14	9.89	33.72	71.43
	Late	2006	49.98	1	-	49.98	49.98
	Late	2009	40.48	13	9.89	26.29	52.11
	Late	2010	33.18	4	3.92	28.97	37.48
	Late	2011	42.70	17	8.42	29.57	54.74
<b>Roughness (dB re 1 m<sup>2</sup>/m<sup>3</sup>)*</b>	Early	2006	1.88	9	0.85	0.70	3.27
	Early	2007	0.92	39	0.36	0.46	1.75
	Early	2008	0.77	7	0.22	0.56	1.19
	Early	2009	0.87	38	0.53	0.37	2.63
	Early	2010	3.10	12	6.48	0.29	23.52
	Early	2011	1.91	18	1.15	0.69	5.05
	Late	2006	1.49	1	-	1.49	1.49
	Late	2009	0.92	14	0.71	0.46	2.75
	Late	2010	4.45	7	2.09	2.13	7.82
	Late	2011	1.59	18	0.85	0.50	3.52

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Table 2. Summary of results from the generalized linear mixed effects models (GLMM) investigating the effect of maturity state and diversity in maturation stages on school descriptors. Parameter estimates and associated test statistics and p-values are presented for the difference between early and late pre-spawning period, and low and high Maturity Diversity Index (MDI), respectively. The effect of depth in the area of sampling is the covariate in the models. Note that the parameter estimates are on the scale of the link function. Year-days > 100 are not included for the two models.

Response variable	Predictor	df	Level	Parameter			
				estimate	t-value	p-value	
<b>Packing density (ind/m<sup>3</sup>)</b>	Maturity		Early	1.053			
		163	Late	1.521	2.018	0.045	
	Covariate (depth)	163		-0.046	3.071	0.003	
	MDI		Low	0.030			
		163	High	0.947	4.473	< 0.001	
	Covariate (depth)	163		-0.029	2.159	0.032	
	<b>Vertical extension (m)</b>	Maturity		Early	1.655		
			163	Late	1.507	1.905	0.059
Covariate (depth)		163		0.004	1.395	0.165	
MDI			Low	1.958			
		163	High	1.632	4.674	< 0.001	
Covariate (depth)		163		< 0.001	0.173	0.863	
<b>Mean depth (m)</b>		Maturity		Early	2.468		
			163	Late	2.535	1.775	0.078
	Covariate (depth)	163		0.015	10.369	< 0.001	
	MDI		Low	2.394			
		163	High	2.493	2.748	0.007	
	Covariate (depth)	163		0.016	10.718	< 0.001	
	<b>Distance from bottom (m)</b>	Maturity		Early	0.164		
			163	Late	-0.252	2.703	0.008
Covariate (depth)		163		0.053	12.885	< 0.001	
MDI			Low	0.292			

			163	High	-0.039	2.4200	0.017
	Covariate (depth)		163		0.053	12.293	< 0.001
<b>Circularity (%)</b>	Maturity			Early	3.588		
			104	Late	3.561	0.420	0.675
	Covariate (depth)		104		0.004	0.888	0.377
	MDI			Low	3.398		
			104	High	3.567	2.559	0.012
	Covariate (depth)		104		0.006	1.445	0.151
<b>Roughness (dB re 1m<sup>2</sup>/m<sup>3</sup>)</b>	Maturity			Early	-5.774		
			154	Late	-5.835	0.355	0.723
	Covariate (depth)		154		-0.025	2.423	0.017
	MDI			Low	-6.800		
			154	High	-6.110	3.695	< 0.001
	Covariate (depth)		154		-0.006	0.646	0.519

Table 3. Summary of cod stomach content from gillnet samples during early and late pre-spawning period from 2006 to 2011 for cod length > 50 cm and < 50 cm. ‘n settings’ denotes number of gillnet settings. No data are available for 2010. ‘Early’ and ‘Late’ refer to early and late pre-spawning periods (see text for details). \*In 2007 1 pollack had 1 herring in its stomach. Mean±SD.

Year	Period	n settings	Mean n cod in catch	n herring in stomachs	n empty stomachs	Mean n cod in catch	n herring in stomachs	n empty stomachs
				<b>Cod size &gt; 50 cm</b>				
2006	Early	2	1.50 ± 0.71	2	1	2.00 ± 1.41	0	2
2006	Late	3	3.67 ± 2.89	2	2	1.63 ± 2.89	0	0
2007*	Early	6	2.00 ± 1.34	2	2	3.00 ± 3.52	0	3
2008	Early	2	3.00 ± 1.41	2	2	0.50 ± 1.00	0	2
2008	Late	6	4.33 ± 2.80	17	6	4.33 ± 5.51	0	0
2009	Late	1	1.00 ± -	0	1	2.00 ± -	0	0
2011	Early	2	1.50 ± 0.71	5	1	6.50 ± 2.12	4	5
				<b>Cod size &lt; 50 cm</b>				

Table 4. *Clupea harengus*. Summary of herring biological parameters from gillnet samples. Mean±SD.

<b>Year</b>	<b><i>n</i></b>	<b>Length (mm) mean</b>	<b>Weight (g) mean</b>	<b>K mean</b>
2006	301	313 ± 15	271 ± 30	0.88 ± 0.08
2007	179	306 ± 18	253 ± 49	0.87 ± 0.10
2008	307	312 ± 20	251 ± 54	0.81 ± 0.09
2009	464	322 ± 18	293 ± 54	0.87 ± 0.12
2010	612	319 ± 18	260 ± 45	0.80 ± 0.08
2011	911	305 ± 29	217 ± 63	0.75 ± 0.10

## Figures

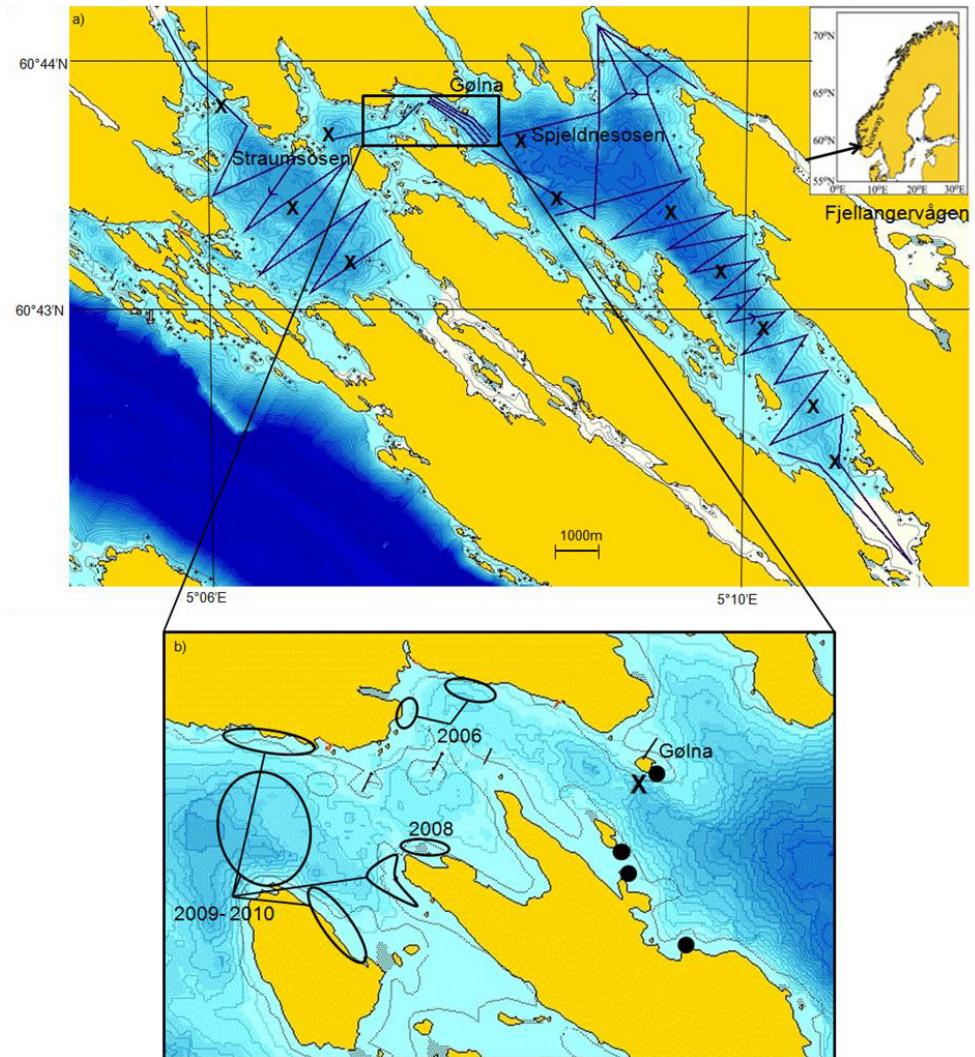


Figure 1. Map of Lindåspollene, south-western Norway showing; a) pre-defined transect grid carried out during 2006 to 2011 to investigate the distribution of herring schools. X denotes positions for CTD stations, b) the main study area; with solid circles denoting herring gillnet positions, and lines denoting predator nets. Open ellipses denote documented spawning grounds and X marks the main CTD station.



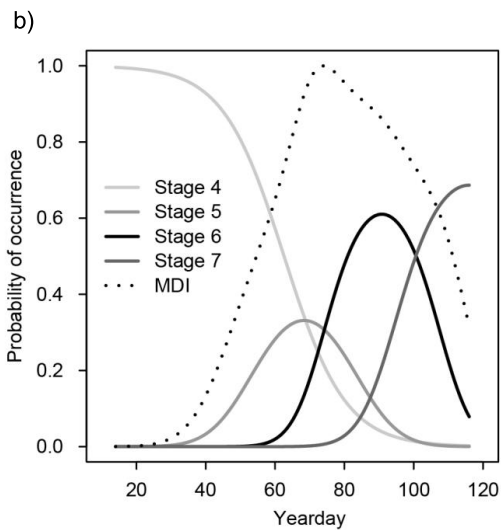
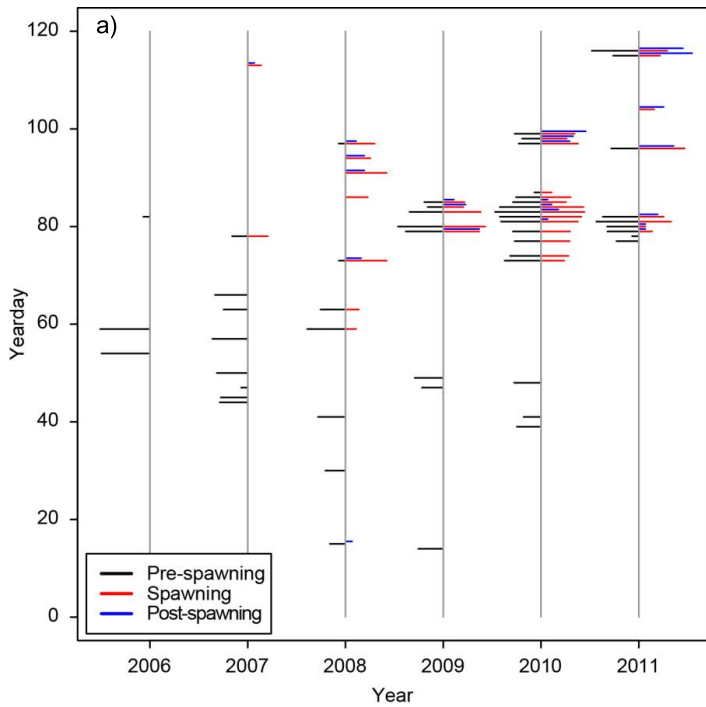


Figure 2. a) Overview of the biological sampling data from 2006 to 2011. Observations of pre-spawning (stage 1-5), spawning (stage 6) and post-spawning (stage 7-8) herring, b) The solid lines show the probabilities of finding a given maturation stage of herring depending on

time of the year, where day 0 represents yearday 1 (January 1<sup>st</sup>). The dotted line shows the MDI describing the potential diversity in maturation stages within a school (see text for further explanations).

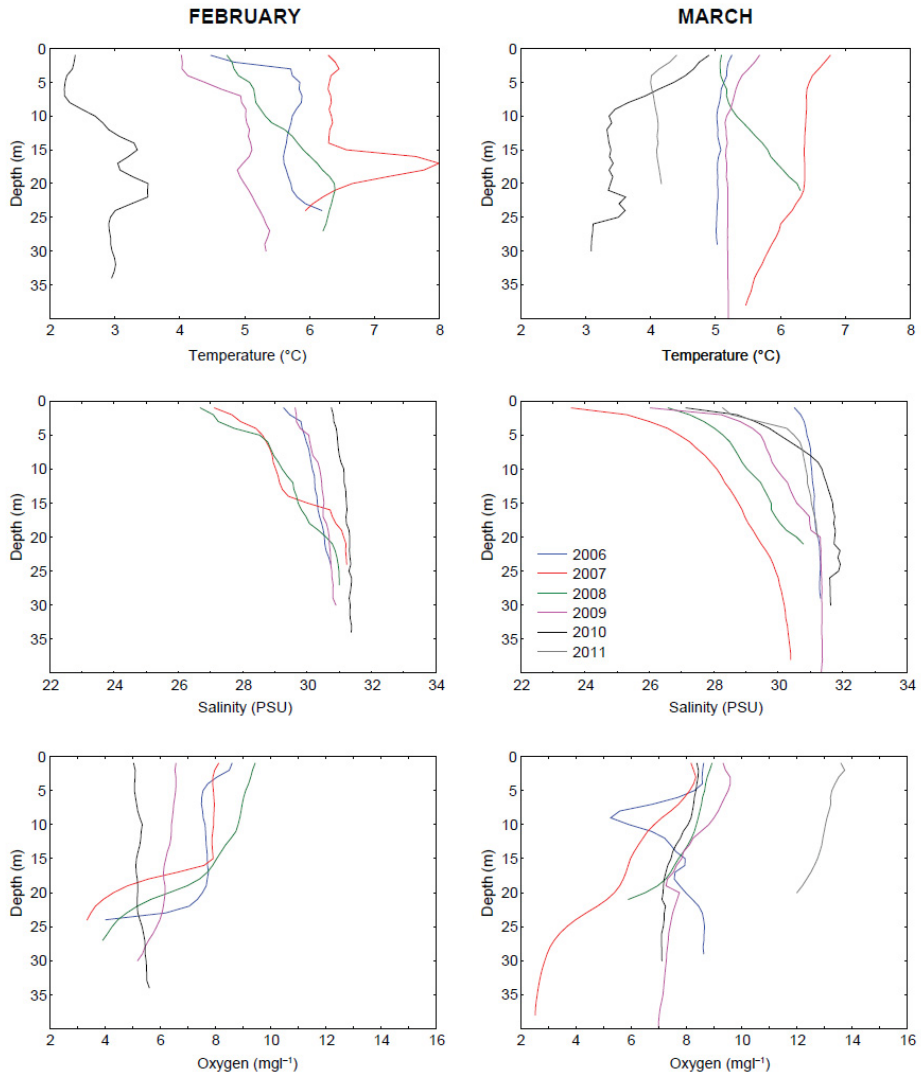


Figure 3. CTD profile taken between yearday 41-53 from 2006 to 2010 (February), and for all years between yearday 72-89 (March).

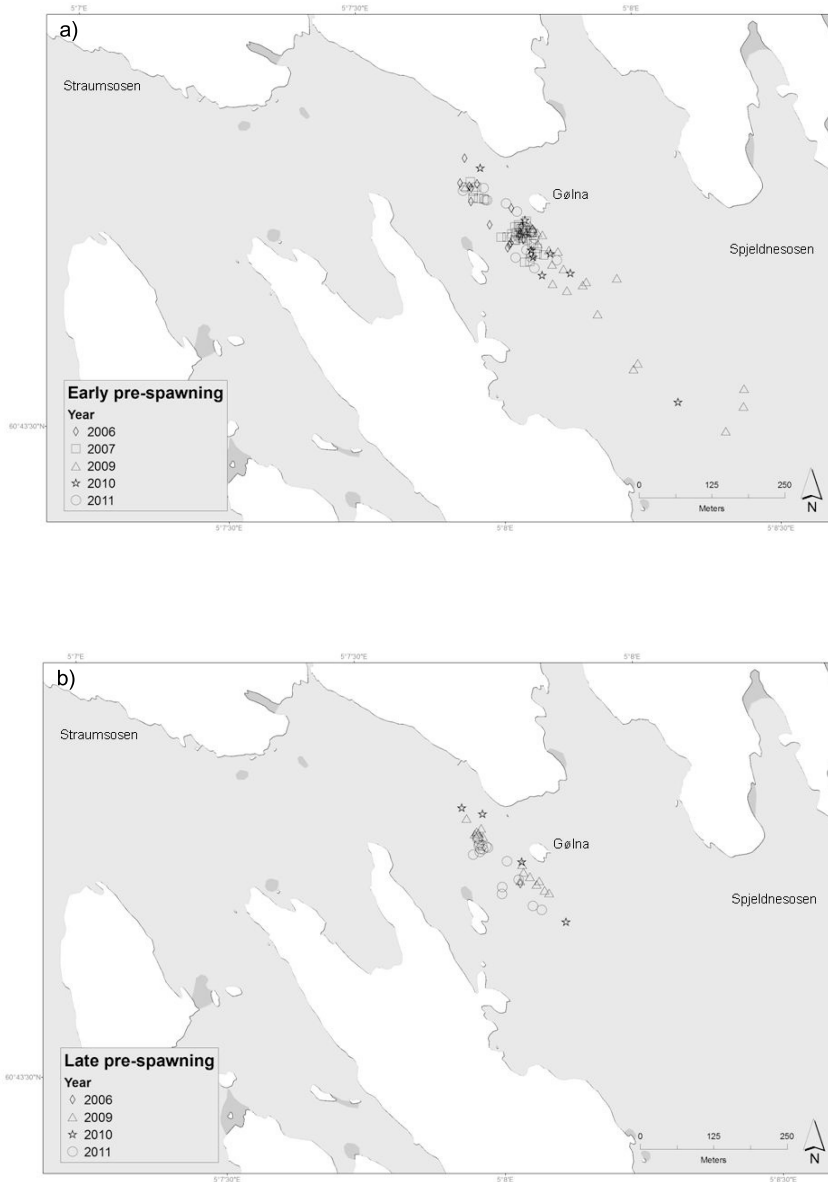


Figure 4. Distribution of school observations from 2006 to 2011 a) early pre-spawning period, b) late pre-spawning period. Note that 30 school observations from the early/late pre-spawning period in 2008 to 2011 are not included due to lack of position data.





Illustration: Åse Husebø

# Acoustic Tagging: A Suitable Method for the Study of Natural Herring Behavior Around Spawning?

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## 1 Introduction

Herring schools can be studied by standard acoustic methods, but to understand the relationship between the individual and school levels as well as the interactions between subpopulations of herring, it is essential to learn more about individual herring behavior. Acoustic tagging has successfully been used to track individual fish of various species, but herring are highly sensitive to being handled and are therefore not easy to tag. In this study, we tagged herring with acoustic transmitters to track prespawning and spawning individuals. The conditions for a tagging experiment were ideal because the herring remained in a single school (>100,000 fish) for more than 1 mo within an area of ~200 m<sup>2</sup> in the sheltered semienclosed Lindåspollene basins (Johannessen et al. 2009). This is a small (7-km<sup>2</sup>) well-defined ecosystem in western Norway, which comprises 3 distinct 60- to 90-m-deep basins containing numerous islets along with several sheltered sites. Here we evaluate whether acoustic tagging is a suitable method for the study of the natural behavior of herring around spawning.

## 2 Tagging Process

Herring were caught individually by jigging from the *R/V Hans Brattstrøm* in February in two seasons. This demanded a high effort lasting for ~4 days because herring seldom feed before spawning (Nøttestad et al. 1996). The fish were kept in lidded holding tanks (500 l) onboard the vessel for ~3 h before being tagged. Fish with signs of injuries or abnormal swimming were sorted out. To minimize handling time, three to four persons took part in the tagging process: 1) each fish was

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captured by a portable net fitted with soft plastic material to avoid damage; 2) it was then held carefully to avoid scale loss (eyes were covered); and 3) the tag was inserted surgically in the abdomen just behind the pelvic fins. The wounds were closed with histoacryl (0.1 ml). The whole procedure took a maximum of 1 min. The fish were left to recover for 3-4 h in a lidded tank (500 l) with circulating seawater and were monitored continuously. Total length of all tagged fish was measured and lost scales were sampled for age determination; for fish that were sorted, the stage of maturity was also determined (see Mjanger et al. 2007). If neither signs of injury nor abnormal swimming was observed, the fish were released at the site where they had been caught. A total of 45 herring (length 28-35 cm, age 4-12 yr) were tagged in the course of the 2 experiments.

## 2.1 Acoustic Tags and Receivers

Two types of acoustic transmitters were used during the two seasons: 1) 17 V9 coded transmitters (V9-1H: length 24 mm, weight in water 2.2 g; V9-2H: length 29 mm, weight in water 2.9 g; Vemco Ltd., Halifax, NS, Canada; <http://www.vemco.com/products/receivers/vrap.php>), and 2) 28 Thelma Biotel (Trondheim, Norway) acoustic transmitters, of which 19 were LP-7.3 mm (length 18 mm, weight in water 1.2 g) and 9 were depth transmitters (ADT-9-SHORT, length 34 mm, weight in water 3.3 g).

On the basis of the results from pilot studies, VR2 receiver units (Vemco Ltd.; see Skilbrei et al. 2009) were moored at 6 sites in Lindåspollene, covering a total range of 1,500 m from the innermost to the outermost location. The receivers were moored to a weight on the seabed and buoyed to a depth of ~10 m. The depth at the receiver sites ranged from 10 to 70 m. The circular detection area of the VR2 had a maximum practical range of 200-400 m.

For more detailed tracking of behavior, a Vemco radio acoustic position (VRAP) real-time system was used (Løkkeborg et al. 2002), with the 3 buoys separated by ~150-250 m. The system is estimated to detect signals from acoustic transmitters at a range of 200-800 m and enables individual tracks to be updated every 5-180 s, with an accuracy of up to 1-2 m (<http://www.vemco.com>) depending on the number of fish tracked simultaneously, type of transmitter, hydrographical conditions, and background noise. The buoys were deployed in a herring spawning area, which was identified by observations of diving eider ducks, herring roe in the stomachs of sampled cod and haddock, and web cameras.

## 3 Evaluation of the Method

During first season, 17 of ~50 herring caught were tagged and released, including 2 pressure tags. The proportion of tagged fish rose in 2010, with 28 fish tagged and released out of 36 fish caught, including 9 pressure tags. The highest discard rate took place after capture. Of the total number of discarded herring (33 in experiment 1 and 8 in experiment 2), 30 and 6 fish, respectively, were discarded before tagging and only a few fish were discarded after tagging (3 and 2, respectively).

The acoustic tags enabled prespawning herring to be reliably tracked to a maximum distance of 400 m from the buoys for up to 90 days. In the first season, we evaluated whether the recordings were in accordance with the expected natural movement pattern of herring. Several types of activity patterns were identified. Five tags that repeatedly transmitted signals from a fixed position and depth were interpreted as representing dead fish. Three tags transmitted signals for ~1 mo, after which contact was lost, and these were interpreted as representing either dead fish or signals lost in other ways. The rest of the tagged fish appeared to behave normally. Nine fish remained within the



relatively stationary main prespawning school for 1-3 mo after being tagged, with shorter or longer excursions to nearby localities, including the spawning site at depths of 0-20 m. This suggests that the fish had spawned, with the high level of activity in the upper layers displayed by some fish late in the period indicating postspawning feeding (Nøttestad et al. 1996). The tagged herring also performed vertical migrations (VRAP and VR2 data) covering the whole recorded water depth.

## 4 Conclusions

To the best of our knowledge, this is the first time that herring have been successfully tagged with internal acoustic transmitters of these sizes. The condition of the fish should always be evaluated before and after tagging, and scale loss must be minimized. Most discards were after capture and a few fish were discarded after tagging. The prespawning period in February, with large and developing gonads, is believed to be a vulnerable period for the tagging of herring, but the low temperatures (1-3°C) may have been favorable for tagging (see Krieger 1982). Although some individuals died or their signals were lost for other reasons, behavior that was interpreted as representing natural herring behavior was monitored in more than half of the fish for several weeks after tagging. These data will have to be analyzed in greater detail to evaluate whether the behavior was affected in any way by the tagging process. Acoustic receivers ought to be located at sites where there is a low risk of interfering sources of sound, and the distances between receivers need to be finely tuned and optimized to the distance of detection to avoid double detections. This new miniaturized acoustic tagging methodology may help us better understand the relationships between the behavior of individual herring and of schools.

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Illustration: Åse Husebø

# Tracking individual herring within a semi-enclosed coastal marine ecosystem: Meso-scale horizontal and vertical dynamics from pre- to post-spawning

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## ABSTRACT

Horizontal and vertical movement patterns of individual herring (*Clupea harengus* L.) inside a 7 km<sup>2</sup> landlocked fjord were studied prior to, during and after spawning using acoustic tags and a network of ultrasonic receivers. Altogether 24 fish were successfully tagged and followed for up to 60 days within the poll. During the pre-spawning period all herring stayed relatively stationary close to one receiver but with marked and predictable diel vertical migrations (DVMs). As maturation progressed, herring gradually moved to the assumed spawning grounds and generally stayed higher in the water column with a smaller depth difference between day and night. In the last phase of the study assumed to include spawning the individuals more frequently shifted between the receivers and after deep dives that could represent spawning events, they eventually moved to the outer basin close to the system outlet. Within this general movement pattern, there was individual variability in both horizontal and vertical positioning that increased over time. The results indicate that within a relatively short time span there was a change from a situation with predictable spatial positioning and strong school coherence to a situation with high individual variability that could reflect variable individual maturation states.

KEYWORDS: Herring · Spawning · Individual behaviour · Horizontal dynamics · Vertical dynamics · Tagging · Acoustics

## INTRODUCTION

Herring (*Clupea harengus* L.) is an obligate schooling fish, living in a constant context of social interactions throughout all its life stages (Blaxter & Hunter 1982). The collective behaviour of a school is the output of individual fish balancing internal motivation (such as hunger, fear and reproduction), factors of environmental influence (such as predation, food, temperature and light) and local stimuli from neighbouring individuals (Pitcher & Parrish 1993, Parrish & Edelman-Keshet 1999). How the different factors are balanced varies according to the life history situation and the ecological context (Nøttestad et al. 1996, Pitcher et al. 1996).

Atlantic herring spawn up to 10-15 times during a lifetime (Blaxter & Hunter 1982, Slotte 1999). During the spawning period the priorities for herring change markedly over a short time span (Nøttestad et al. 1996). The whole period of pre-spawning, spawning and post-spawning involves multiple state-dependent trade-offs between predator avoidance, reproduction and feeding that influence spatial selection of pre-spawning and spawning sites, vertical dynamics and time of spawning (Nøttestad et al. 1996, 2004, Slotte & Fiksen 2000, Axelsen et al. 2000, Skaret et al. 2003). Norwegian spring spawning (NSS) herring spend 1-7 days at the spawning grounds (Johannessen 1986, Axelsen et al. 2000, Skaret et al. 2003). The location of the spawning site is determined by factors like substrate/topography, depth, temperature, oxygen conditions and currents (Runnström 1941, Iles & Sinclair 1982, Sætre et al. 1998, Holst et al. 2004). Herring spawn on traditional spawning grounds meeting the suitability criteria (e.g., Hourston 1982, Wheeler & Winters 1984), and local herring in the semi-enclosed coastal marine system Lindåspollene in south-western Norway has high fidelity to a pre-spawning site providing a vertical escape route (Langård et al. submitted a).

Herring use the vertical dimension actively during predator avoidance (Axelsen et al. 2000, Skaret 2007, Johnsen & Skaret 2008), and also perform distinct diel vertical migrations (DVMs) during large parts of the year (Huse & Ona 1996, Mackinson et al. 1999). During spawning, the vertical distribution is particularly dynamic since herring adapted to a pelagic life spawn demersally (Runnström 1941). The bottom could be associated with high predation risk (Johnsen & Skaret 2008), and herring seem to prefer to stay above the demersal zone to minimise risk of predation (Axelsen et al. 2000, Johnsen & Skaret 2008). The emergent collective behaviour resulting from the trade-off between reproduction and predator risk may

lead to advanced schooling patterns (Vabø & Skaret 2008). Still, neither the vertical nor the horizontal behaviour of individuals within the setting of the collective is known.

To study herring behaviour at relevant scales within their natural environment is a challenge (Nøttestad et al. 2004). Studies of herring behaviour have typically focused on schools using active acoustics (Nøttestad et al. 1996, Mackinson 1999, Axelsen et al. 2000, Skaret et al. 2003). Such an approach provides information on the school level, but individual behaviour and trade-offs have to be inferred from the observed collective output. Recently, small and light acoustic tags have been developed that can be inserted into small pelagic fish (Arnold et al. 2002) allowing for behavioural studies of individual fish. Individual herring are difficult to tag due to scale loss during handling (Harden Jones 1968, Jacobsen & Hansen 2004), but we have succeeded in applying acoustic tags in herring permitting tracking of individual fishes (Langgård et al. 2012, Eggers 2013). A prerequisite for such studies is that individuals can be followed over extended periods of time, which is difficult in open ocean systems. In Lindåspollene covering only about 7 km<sup>2</sup>, a local herring population is present at least during large parts of the year (Lie et al. 1978, Aksland 1983, Langgård et al. submitted a). The system is sheltered from heavy weather and is ideal for tagging studies and also well known from previous studies.

Here we study individual herring behaviour in Lindåspollene during the whole period from pre- to post-spawning. Based on information from individual tags we aim at describing the horizontal and vertical distribution and movements of individual herring throughout the spawning period in relation to the change in maturation state recorded from biological samples.

## **MATERIALS AND METHODS**

### **Study area**

Lindåspollene is a small semi-enclosed ecosystem in south-western Norway comprising three 60-90 m deep basins (see Lie et al. 1978), with a main sill connecting to the outside fjord (Fig. 1). The study site is protected from severe wind and wave conditions and is suitable for experimental studies.

## **Tagging and release**

Experimental fish were captured by jigging from the RV “Hans Brattstrøm” (24.3 m long and 6.5 m wide; 79 GRT) in 2010 (yearday, YD, 39-42). Only uninjured specimens were used (see Langård et al. 2012). In all, 28 herring were tagged with small acoustic Thelma Biotel transmitters (Vemco Ltd, Shad Bay, Nova Scotia). The transmitters were of 2 types: either individually coded (Low Power (LP) LP-7.3 mm, n = 19) providing only tag ID, or Acoustic Depth Transmitters (ADT) (ADT-9-SHORT (SHORT refers to length of transmitter), n = 9) providing both ID and depth. Coded (length 18 mm) and depth transmitters (length 34 mm) weighed 1.2 g and 3.3 g in water, respectively. The transmitters had a random delay of 60-180 sec between transmissions to minimize signal collisions (average 120 sec), allowing a large number of fish to be tracked on the same frequency (69 kHz). The coded transmitters had an expected battery life of ~5-8 months, and the depth transmitters ~4.5 - 7.5 months. The herring tagged with ADT and LP tags were of similar length ( $32.2 \pm 1.4$  SD and  $32.6 \pm 1.4$  SD cm) and age ( $9.0 \pm 2.1$  SD and  $9.0 \pm 1.6$  SD years). The investigation was terminated on yearday 100. The herring should ideally have been observed over an even longer time to reveal whether they eventually left Lindåspollene, but the acoustic receivers were unfortunately not available after that time.

Transmitters were surgically inserted in the abdomen of the fish as described in Langård et al. (2012). Individuals were measured to the nearest cm and placed ventral side up in a net fitted with soft plastic material to avoid damage to the herring and to remove scales for age determination (4-12 years). A 10 mm long incision was made posterior to the pelvic fin, and a transmitter sterilized in surgical spirit was carefully inserted forward into the peritoneal cavity in the abdomen just behind the pelvic fins. The incision was closed with histoacryl tissue adhesive (0.1 ml) to prevent it from opening. The whole procedure took a maximum of 60 sec. Fish were then transferred to a lidded tank (500 l) with circulating seawater for 3-4 h for recovery and continuous observation until no visible effects of tagging like injury or abnormal swimming were seen. All fishes were finally released in the area of capture. The experiment and tagging procedure was approved by the Norwegian committee for the use of animals in scientific experiments (FDU).

## **Acoustic receivers**

Stationary acoustic receivers (VR2, Vemco Ltd) were moored at 5 geographical locations in Lindåspollene (Fig. 1), covering a total range of approximately 2500 m from the inner to the



outer location. The receivers were placed at specific locations based on past studies in the poll; one close to the pre-spawning area, another close to the spawning area and the rest at possible inlets/outlets (Østvedt et al. 1973, Aksland 1983, Johannessen et al. 2009). The receivers recorded ultrasonic signals transmitted within a circular detection area, varying between 200 and 400 m depending on ambient oceanic/weather conditions and bottom topography (see Skilbrei et al. 2010). The receivers were positioned taking into consideration the bathymetry, shadow zones and distance between receivers that could result in overlap, but the system was not calibrated with a range-testing tag. The receivers were moored to a weight on the seabed, and kept at a depth of about ~10 m by a float. The depth at the receiver sites ranged from 10-70 m. The receivers were deployed simultaneously as herring were tagged and taken up on yearday 100.

### **Biological and hydrographical sampling**

Biological samples of herring were obtained by gillnet catches in the area (Fig. 1). Herring were sampled in February to April (YD 39, 41; n = 8, YD 73-74, 77, 79; n = 255, YD 81-87; n = 566, YD 97-99; n = 268) using monofilament gillnets; 25 m long by 4 m high, with stretched mesh sizes of 24-36 mm. Altogether 16 gillnet samples were acquired during the study period. Individual herring were measured for total length (L) to the nearest 0.5 cm below and scored for gonad maturity stages according to an 8-point scale based on macroscopic visual inspection (for details see Mjanger et al. 2013, Langård et al. submitted a). CTD casts (STD/CTD, model SD204, SAIV) were taken for temperature, salinity and oxygen at the pre-spawning area (Fig. 1). Each measurement was rounded to nearest whole meter and averaged over the samples during each of the 3 defined periods (see next section). Spawning of herring was documented by underwater video camera recordings of herring spawn and eggs in predator stomachs.

### **Analyses**

To study individual behaviour in relation to maturation and spawning, we divided the acoustic detections into 3 periods according to average gonad maturity state derived from the gillnet samples. The periods were defined as follows: Pre-spawning (P1): first day when proportion of individuals with GMI 4 (maturing) was the highest in the sample, Ripe (P2): first day when proportion of GMI 5 (maturing) was the highest and Spawning (P3): first day when proportion of GMI 6 (spawning) was the highest. Also a Spent category was defined as the first day when the proportion of GMI 7 was the highest, but this period only included one day

of recordings and was omitted from the analyses. To take into account the variable sampling effort, we used bootstrapping and defined the periods 1000 times leaving out one random gillnet sample each time. We then used the average value ending up with the following ending day for each period (YD  $\pm$  SD): 50  $\pm$  5.65SD for P1, 78  $\pm$  0.50 for P2 and 99  $\pm$  0.23 for P3.

As a criterion for inclusion of single received signals in the analyses, a minimum of 2 received signals per day from a specific tag ID from one or adjacent receivers was set as a requirement. In addition, recordings from 4 ID tags were excluded from the analyses. Two of these ID tags consistently transmitted signals from the maximum recording depth (51 m) and at one specific receiver; these tags were interpreted as being lost or inside deceased herring. From 2 other ID tags, only scattered signals were recorded with long periods without recording signals, and the last received signals were from the maximum depth.

All statistics were performed using R version 3.0.0 (R Development Core Team 2013, <http://www.rproject.org>). The vertical distributions over 24 h were compared among the 3 periods P1, P2 and P3 by using a generalized additive model (GAM) from the mgcv library of R (Wood 2006). The R syntax for this model was:

```
gam(Depth~s(Hour) + factor(Period) + s(Hour, by=Period) + s(ID, bs='re'),  
family='quasipoisson')
```

where Depth is the response variable describing depth (m) of each individual, Hour is a continuous predictor describing time (24 h), Period is a categorical predictor with the 3 levels describing maturity (P1, P2 and P3). The variable ID contains a unique number for each fish and is included to account for the random effect of individuals. The vertical distribution throughout the observational period was also investigated to see how mean depth in general and the difference in mean depth between day and night changed over the season. We used both a GAM and a linear mixed effect model (LME) for this purpose. For the GAM, we used the same syntax as in the above model but with yearday as a continuous predictor and Light as a categorical predictor with the two levels day and night representing the light conditions at the time of sampling. In this analysis, samples taken at civil twilight (when the sun is between 0 and 6° under the horizon) were excluded from the data set. This was done since we in this model, in contrast to the one described above, wanted to avoid the time when fish moves up and down. In addition to the GAM, we used the LME to investigate if the difference between

day and night samples changed between the pre- and spawning period. The R syntax for the LME was:

```
lme(Depth~Period*Light, random=~+I|ID, cor=corAR1())
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where the variables are the same as described in the previous models but with Period only including the levels P1 and P3 to make model interpretation as simple as possible.

For the fish with the depth tags we compared the vertical movement within each of the 3 periods; pre-spawning, ripe and spawning by using the same type of LME as described above, but with the Sum of vertical meters moved for each fish as the response variable and only with Period as predictor in the model. We also evaluated the horizontal movement for the same fish. However, in the horizontal movement the response variable was recorded as the number of receiver changes for each fish. Thus, we used the same type of mixed model approach with autocorrelation but used the *glmmPQL* function from the MASS library of R (Veneables & Ripley 2002) due to the need of poisson regression for count data.

## RESULTS

### Horizontal distribution

Of the total of 28 fish tagged, 24 fish met the criteria for being included in the analysis. The results of the poisson regressions (Fig. 2) show that there is a significant reduction in number of fish with yearday at receiver 1 (pre-spawning area) (GLM;  $F_{1,59} = 90.40$ ,  $p < 0.01$ ), a maximum number of fish at receiver 2 (spawning area) at day 76 (GLM with second order polynomial;  $F_{2,58} = 38.03$ ,  $p < 0.01$ , significance of second order term;  $F_{1,58} = 56.30$ ,  $p < 0.01$ ), a significant increase over time at receiver 3 (primary outlet) (GLM;  $F_{1,59} = 174.11$ ,  $p < 0.01$ ), and no significant change over time at receiver 4 (secondary outlet) ( $F_{1,59} = 0.65$ ,  $p = 0.42$ ). No recordings were made at receiver 5. In general, the gathering around a single receiver is strongest in a relatively long period between yearday 40 and 60 and in a short period around yearday 70 (just before spawning is assumed to start). In addition to these general trends in distribution, the dynamics around yearday 60 is worth attention. At this time there was a significant drop in number of individuals at the pre-spawning area, and a subsequent leap at the spawning area. Interestingly, the short period with high number of individuals (10-13) at the spawning area was immediately followed by a 5-day period with low numbers (5-7). During this period, 8 fish were in fact not detected by any receiver. During the same period,

some individuals started to occur at receiver 4, indicating that this first break-out period around yearday 60 could be an exploratory phase for some of the individuals. Furthermore, there was a significant lower number of shifts between the receivers in P1 in relation to P2 and P3 (GLMM;  $t = 3.88$ ,  $df = 8$ ,  $p < 0.01$ , and  $t = 4.93$ ,  $df = 8$ ,  $p < 0.01$ , respectively, Fig. 3), whereas P2 and P3 were not significantly different (GLMM;  $t = 0.51$ ,  $df = 8$ ,  $p = 0.63$ , Fig. 3).

### **Vertical distribution**

Herring showed DVMs throughout the tracking period staying significantly deeper at daytime compared to night (GAM;  $t = 242.50$ ,  $p < 0.01$ ; Fig. 4). However, there was a general decrease in depth distribution over the study period ( $F = 873.23$ ,  $p < 0.01$ ), except for a period prior to yearday 90 when depth distribution again increased. The decrease in depth distribution was confirmed when comparing different time periods (Fig. 5). Herring were detected significantly deeper during P1 than during both P2 and P3 (GAM;  $t = 20.19$ ,  $p < 0.01$ , and  $t = 99.78$ ,  $p < 0.01$ , respectively). The two periods P2 and P3 were also significantly different from each other (GAM;  $t = 96.54$ ,  $p < 0.01$ ). The effect of Hour (time of day) was also significant ( $F = 35.75$ ,  $p < 0.01$ ), meaning that the general change in depth over 24 h was significant. The LME confirmed that the differences in depth distribution between day and night detections were larger in the pre-spawning than in the spawning period (LME; interaction between Period and Light,  $F_{1,15609} = 716.13$ ,  $p < 0.01$ ). The smallest differences in depth distribution between night and day were detected between yearday 70-80 (Fig. 4), which coincided with the time the fish aggregated in the spawning area (Fig. 2).

In Fig. 6, individual and day-to-day-variability in depth distribution during the 3 defined periods are visualised. The sum of number of vertical meters that each fish moved was significantly higher in P2 compared to P1 and P3 (LME;  $t = 6.41$ ,  $df = 8$ ,  $p < 0.01$ , and  $t = 5.83$ ,  $df = 8$ ,  $p < 0.01$ , respectively (Fig. 7). P1 and P3, were not significantly different (LME;  $t = 0.61$ ,  $df = 8$ ,  $p = 0.56$ , Fig. 7). During P1, the majority of the day time recordings were from 25-50 m depth with individual fish typically using a range of 20-25 m. In P2, depth distribution at both night and day gradually became shallower for all individuals, and the vertical range also decreased. Around yearday 60 a behavioural change to shallower distribution was observed in all individuals. At the end of P2, some herring were for the first time as high in the water column during daytime as night-time. During P3, more unpredictable vertical dynamics were observed. Herring were now commonly found at shallow depths during day time similar to night time, but there were occasional deep day time

dives, some of which were of long duration, and the timing differed between individuals. Notably, the deep dives were followed by a horizontal shift to the primary outlet close to the outlet (Fig. 6). Occurrence of spawning was verified through video observation of eggs in shallow waters (0-15 m) on yearday 85 close to the spawning area (Fig. 1). Predator stomachs contained herring eggs in all 5 samples carried out between yearday 85 to 100.

### **Hydrographical conditions**

The temperature in the upper 10 m showed most variation through the study period, with an increase of almost 2°C between P2 and P3 (Fig. 8). This implied a shift in the thermocline before spawning in accordance with Langård et al. (submitted b). The salinity level was between 27 and 32 (Fig. 8), but lower close to the surface in P2, probably due to fresh water run-off. The oxygen level in the water column ranged between 5 to 8.5 mg L<sup>-1</sup> in the upper 15 m (Fig. 8).

### **DISCUSSION**

This study in a small, semi-enclosed system throughout the spawning period elucidates the spatial decisions of individual herring during phases of varying conflict within and between individuals. Horizontally, herring gradually moved away from the pre-spawning location to the assumed spawning site to end up in the outer basin close to the outlet of the system. Pre-spawning herring showed marked DVMS staying deeper during day time. DVMS gradually decreased over time and herring approaching spawning stayed close to the surface both during day and night with occasional deep dives. The individual variability increased when the herring approached spawning.

The tagging of the herring was successful, with only 4 of the 28 tagged fish discarded from the analyses due to unrealistic behaviour during the 60 day observation period. The results indicated some overlap in coverage between receiver 1 and 2, but this did not seem to significantly influence our observations given the marked positional changes between these receivers over time.

### **Horizontal distribution and movements in relation to maturation state**

The horizontal distribution changed according to the state of maturation. The optimal locations for energy saving and risk reduction during pre-spawning, egg deposition during spawning and feeding during post-spawning should be expected to differ. Herring has

previously been shown to select the same pre-spawning location in Lindåspollene as found here (Langård et al. submitted a). This site is quite deep and leads out to even deeper waters that should provide good opportunities for predator escapement. As maturation progressed the individual herring gradually moved towards the assumed spawning grounds, where the abundance reached a peak on yearday 70.

At the end of the study period, herring were recorded in increasing numbers at the outer part of the poll by the primary outlet. This area could provide good feeding opportunities on zooplankton entering from the more productive outside fjord (Østvedt et al. 1973, Lie & Dahl 1981, Aksnes & Magnesen 1983, Salvanes et al. 1995, Ohman et al. 2004), although some herring have also been found in more southern parts of the poll. The present study could not explore the behaviour past spawning. Herring have earlier after spawning been observed to conduct feeding migrations to the outer basin (Østvedt et al. 1973) and migrate out of the main sill to the outside fjord system (Aksland 1978), but there is little information regarding the extent of this emigration. An interesting possibility is that the increasing number of herring at the outlet is due to spent herring awaiting the situation before leaving in a larger group safer from predation (Pitcher & Parrish 1993, Axelsen et al. 2000).

### **Vertical distribution and movement in relation to maturity state and time of day**

The swimming depth of herring changed throughout the spawning period and with the diel cycle. Pre-spawning herring conducted long DVMs staying deeper during day than at night. Such behaviour has earlier been observed during pre-spawning (Runnstrøm, 1941, Skaret 2007) and is consistent with the general DVM observed in herring (Blaxter & Parrish 1965, Huse & Korneliussen 2000, Cardinale et al. 2003, Nilsson et al. 2003, Jensen et al. 2011). DVM can be a feeding strategy, where the predator movements mirror the movements of the prey (Eshenreder & Burnham-Curtis 1999), but pre-spawning and spawning herring do generally not feed (e.g. Parsons & Hodder 1975, Crawford 1980, Huse & Ona 1996, Slotte 1999) as is also the case in Lindåspollene (Langård et al. submitted a). This makes it crucial to save energy by minimizing swimming and basic metabolism (Huse & Ona 1996). As a pelagic and physostome species (Ona 1990) herring must swim to avoid sinking to the bottom (Huse & Ona 1996, Kaartvedt et al. 2009). Since the negative buoyancy and hence the energy spent to compensate for that increases with depth, there should be a significant advantage for herring to stay close to the surface (Nero et al. 2004). Staying in shallow waters also reduces gas diffusion through the wall of the swimbladder (Fässler et al. 2009). It has been suggested

that herring is only able to inflate the swimbladder by ‘gulping’ atmospheric air at the sea surface (Brawn 1962, Blaxter et al. 1979, Blaxter & Hunter 1982, Blaxter & Batty 1984, Ona 1990, Nero et al. 2004), but observations of air gulping are largely lacking, and we did not observe herring at the surface prior to yearday 70.

If staying close to the surface is an energetic advantage, why was such behaviour only observed during night time? The reason could be that during periods with daylight, herring swim towards darker waters deeper down to reduce the vulnerability to visual predators (Levy 1987, 1990b, Clark and Levy 1988, Rosland & Giske 1994, Cardinale et al. 2003). Herring could also have to trade off additional factors. The temperature close to the surface in the pre-spawning period was less than 3°C (Fig. 8), which is considered to be a low tolerance limit for herring over time (Østvedt 1965). Low temperature could make herring avoid the surface waters, and although herring had a shallow distribution at night they stayed in a narrow vertical range below the thermocline in this period.

Herring gradually ascended, and after yearday 70 at the end of the ripe period and onwards the fish were regularly recorded at the surface. The DVM pattern also changed over time. During the spawning period (P3), herring were commonly found at shallow depths both day and night. There could be several reasons for staying near to the surface closer to spawning. In P3, the temperature was 2°C higher close to the surface than below the thermocline. The increasing surface temperatures could attract herring as warmer waters speed up the physiological processes linked to maturation and spawning (Langård et al. submitted b) and video observations showed that some spawning occurred in shallow waters. Yet, deeper waters could not be explored in the same way, and the occasional deep dives followed by migrations to the outer part of the poll were interpreted as spawning events. The dives could last for several hours and herring seem to be capable of spawning quickly and even in one batch (Bowers & Holliday 1961, Harden Jones 1968, Axelsen et al. 2000).

### **Individual variability**

When herring approached spawning the individual and day-to-day variability in horizontal and vertical positioning increased indicating a more dynamic situation with increased conflicts both within and between individuals. This suggests that not only does the horizontal and vertical positioning gradually change through pre-spawning and spawning period, but also the relationship between the individual and the group. During pre-spawning, herring were

horizontally relatively stationary and although vertically dynamic they following a rhythmic and predictable pattern despite the individual variation in gonad maturity. The coherence in the large group is then likely to be strong and the individuals would be expected to prioritise to keep in contact with the group, while avoiding predator attacks. In the ripe period the ascent around yearday 60 strongly indicated a particularly dynamic period with high individual vertical dynamics closer to spawning and with different state-dependent trade-offs in the individual fish. As spawning approaches, the increased movement and individual heterogeneity in behaviour indicated that the fish to a larger degree behaved as individuals.

## CONCLUSIONS

This study demonstrates that acoustic tracking is an efficient technique to study the behaviour of small pelagic fish like herring *in situ*. The herring in Lindåspollene went through different behavioural phases linked to their maturation state. Both in the horizontal and vertical dimension the individual and day-to-day variability increased when herring approached spawning indicating increased conflicts within and between individuals. Pre-spawning state showed high fidelity to a certain site and stayed within a narrow vertical range below the thermocline at night with a deeper wider range during the day. A combination of energy conservation at shallow waters minimizing gas diffusion and avoidance of the risky surface waters during the day could explain the observed vertical dynamics. In the ripe period, the horizontal dynamics and presumably exploratory behaviour increased and the herring gradually ascended with a decreased vertical range. At spawning the herring generally stayed close to the surface and eventually moved to the primary outlet. To increase the resolution of the spatial dynamics even further, stationary positioning systems (VRAP) that track the positions of each fish in real-time may be employed. Combining information on the micro and meso-scale behaviour will make it possible to address basic ecological questions about the schooling dynamics of pelagic fish.

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## Figures

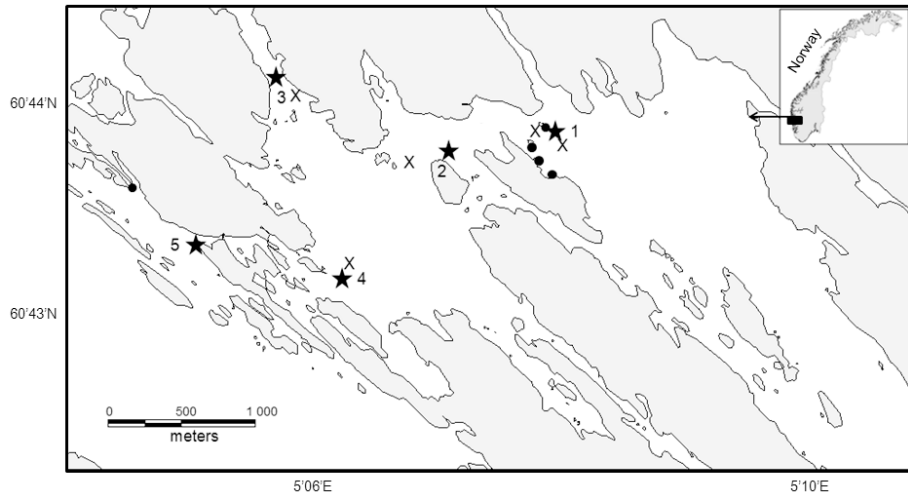


Figure 1. Map over the study area in Lindåspollene. The 5 acoustic receivers are represented by stars. X denotes locations for CTD casts and black filled circles denote herring gillnet locations.

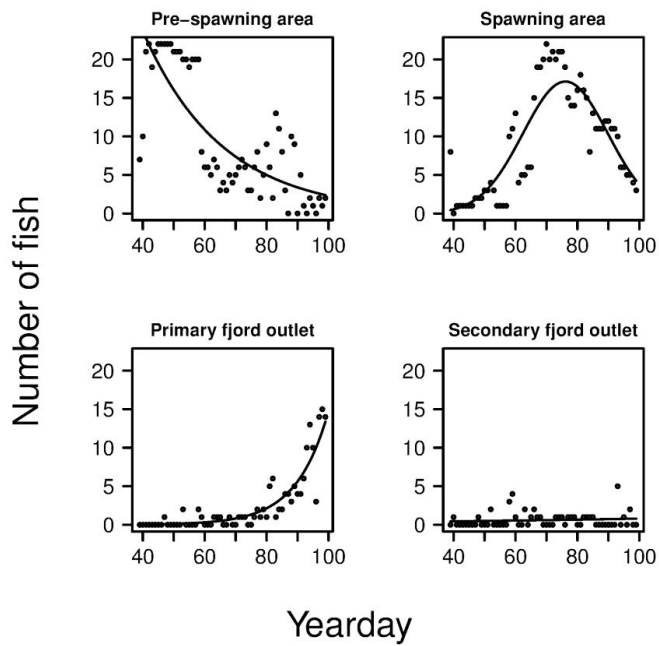


Figure 2. Overview of number of fish observed at the different receivers throughout the study.

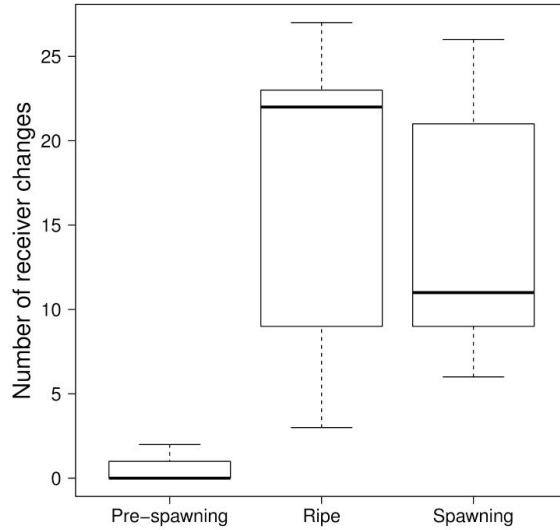


Figure 3. The number of receiver changes the individual fish conducted during the pre-spawning, ripe and spawning period. Values portrayed are the median, 1<sup>st</sup> and 3<sup>rd</sup> quartile, whiskers represent max. and min. values except for outliers.

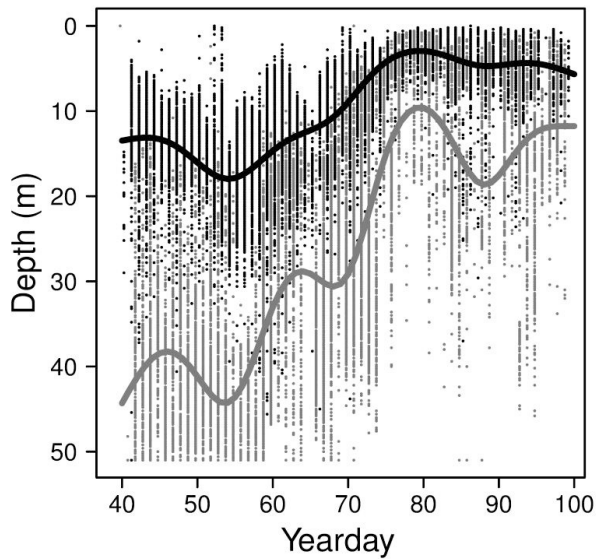


Figure 4. Detected vertical position as a function of yearday based on all tag recordings. Grey dots mark day time recordings and black dots mark night time recordings. The solid lines mark

GAM fitted to day time (grey) and night time (black) data. Note that maximum detection depth was 51 m and actual depth in certain locations may exceed this depth.

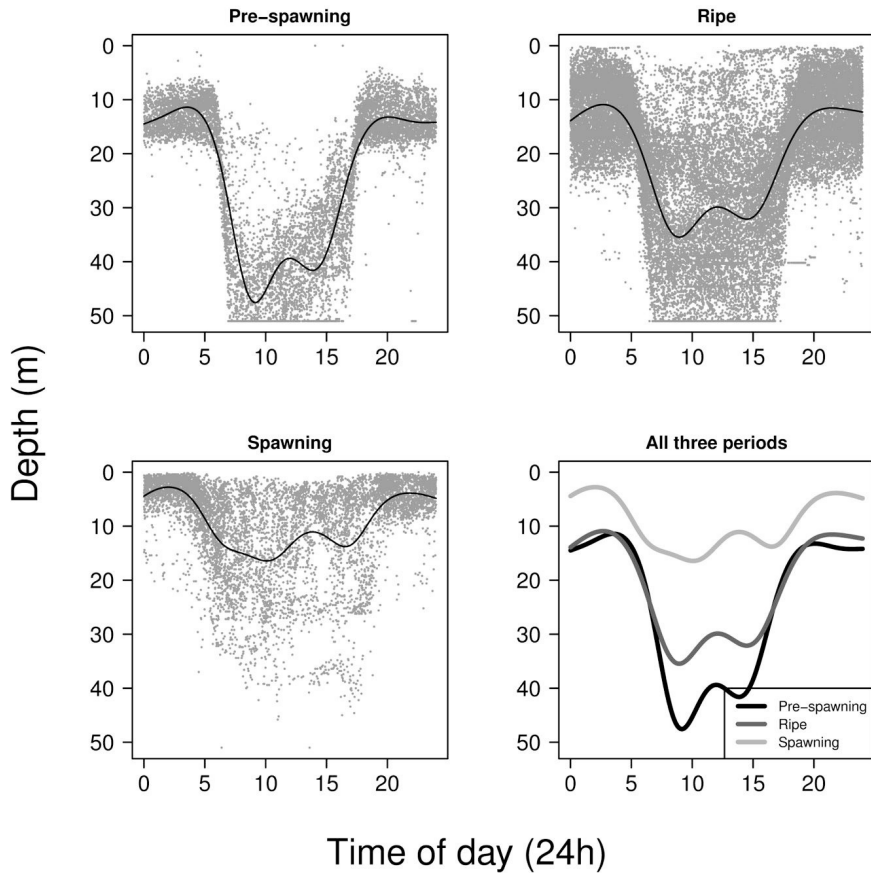
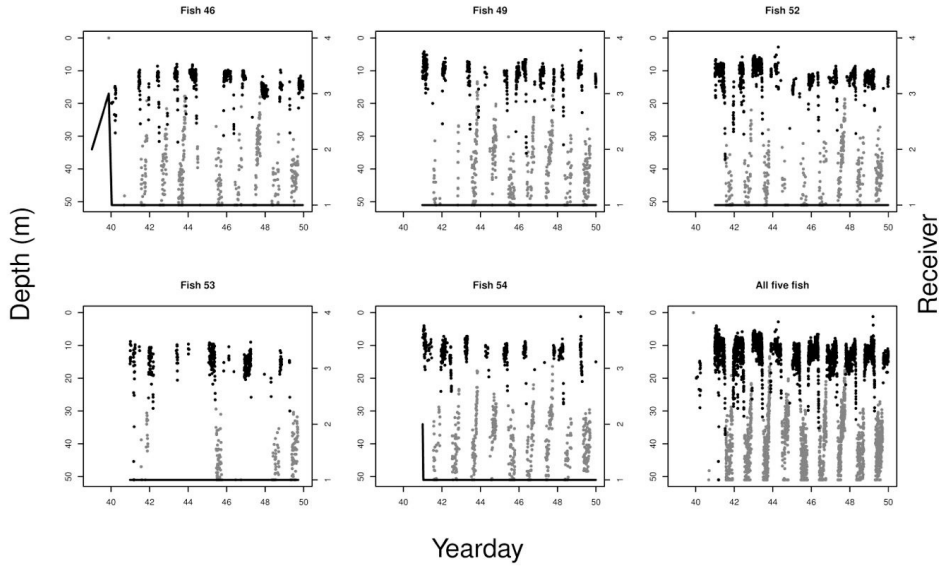


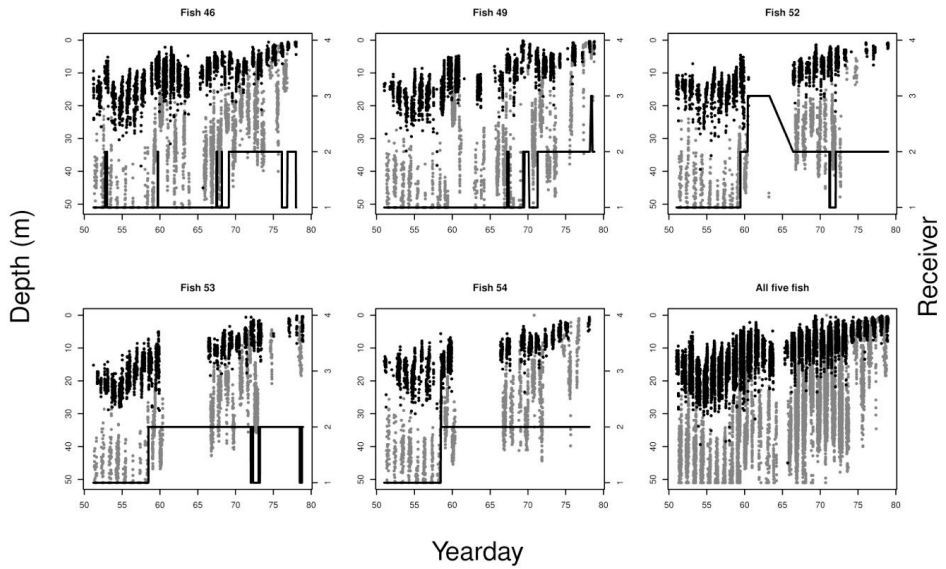
Figure 5. Detected vertical position as a function of time of day based on all herring tag recordings. The separate panels contain detections for the 3 different periods pre-spawning, ripe and spawning. The solid lines mark the fitted GAMs. Note that maximum detection depth is 51 m.

### Pre-spawning



### Yearday

### Ripe



### Yearday



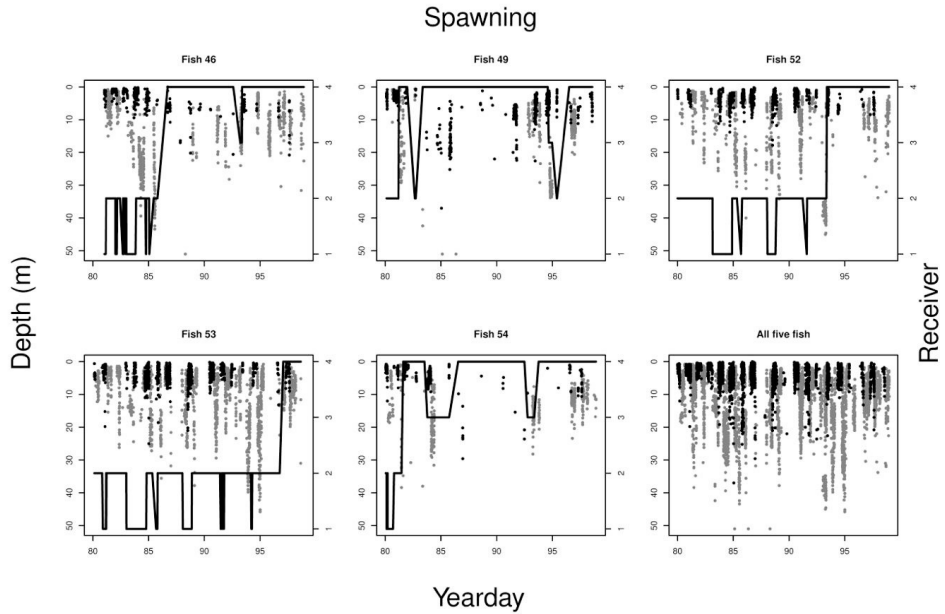


Figure 6. Detected vertical position as a function of yearday during day time (grey) and night time for the different periods based on individual herring tag recordings. The solid line marks the position of individual herring in relation to the different receivers. The separate panels contain detections for the 3 different periods pre-spawning, ripe and spawning.

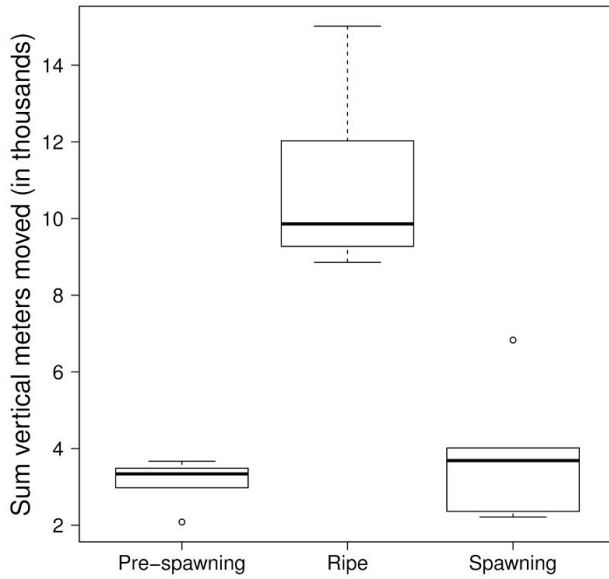


Figure 7. The sum of vertical meters moved for each fish during the 3 different periods, pre-spawning, ripe and spawning. Values portrayed are the median, 1<sup>st</sup> and 3<sup>rd</sup> quartile, whiskers represent max. and min. values except for outliers.

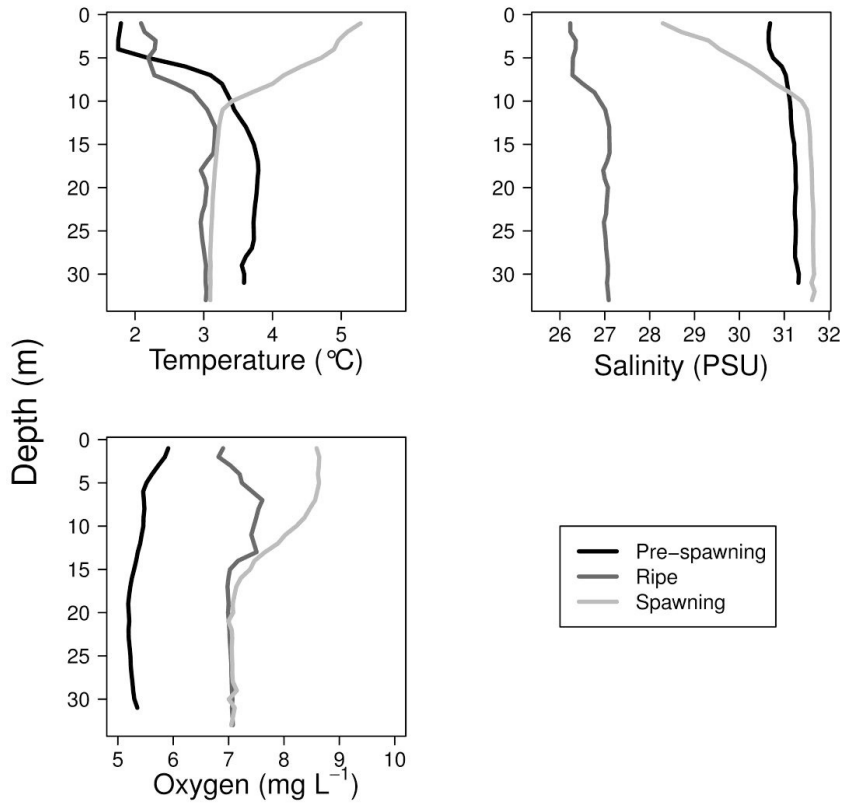


Figure 8. CTD profiles from the pre-spawning area. The separate panels contain the temperature (°C), salinity and oxygen (mg L<sup>-1</sup>) profiles for the 3 different periods; pre-spawning, ripe and spawning.

