Reproductive traits across the Atlantic herring (*Clupea harengus* L.) stock complex

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List of abbreviations

AP: Apoptosis

AW: Atlantic Water

BCH: British Columbia herring

BFH: Balsfjord herring

BW: Blue whiting

CAO: Cortical alveoli oocytes

CNR: Circumnuclear ring

CSH: Coastal Skagerrak herring

D: Maximum depth

DR: Down-regulation

DVM: Diel vertical migration

EDW: Egg dry weight

EDW_{fixed}: Egg dry weight of fixed eggs

EEZ: Exclusive Economic Zone

EOR_N: Early oocyte recruitment reported as numerical production

F: Fishing mortality

F_P: Potential fecundity

GF: General fecundity formula

GLH: Gloppenfjord herring

GSF: Good-seasons females

GSI: Gonadosomatic index

GW: Gonad weight

IMR: Institute of Marine Research

ISSH: Icelandic summer-spawning herring

K: Fulton's condition factor

K_{slope}: Slope of Fulton's condition factor when regressed on TL

L: Large PVOs

L_{50}: Length at first maturity

L_∞: Asymptotic length

LC: Leading cohort oocyte diameter

LPH: Lindås herring

LRH: Lake Rossfjord herring

LVH: Landvik herring

M: Medium-size PVOs

NAC: Norwegian Atlantic Current

NAO: North Atlantic Oscillation

NASH: Norwegian summer-autumn spawning herring

NCC: Norwegian Coastal Current

NCW: Norwegian Coastal Water

NEA: Northeast Atlantic

NEAM: Northeast Atlantic Mackerel

NSAH: North Sea autumn-spawning herring

NSH: North Sea herring (autumn and winter spawners combined)

NSSH: Norwegian spring-spawning herring

NSWH: North Sea winter-spawning herring

NWA: Northwest Atlantic

NwAFC: Norwegian Atlantic Front Current

NwASC: Norwegian Atlantic Slope Current

NwSDW: Norwegian Sea Deep Water

OD: Oocyte diameter

OP: Oogonial proliferation

OPD: Oocyte packing density

P&GSF: Poor- and good-seasons females

PEP: Potential egg production

POF: Postovulatory follicle

PVO: Previtellogenic oocytes

REC: Recruitment

$RF_{P,S}$: Somatic potential relative fecundity

$RF_{P,W}$: Potential relative fecundity

RI: Reproductive investment

S: Small PVOs

Sal: Salinity

SFH: Scotia-Fundy summer-autumn spawning herring

SGH: Sognefjord herring

SRP: Stock reproductive potential

SS: Spawning season

SSB: Spawning stock biomass

T: Temperature

TEP: Total egg production

TL: Total length

TRH: Trondheimsfjord herring

VO: Vitellogenic oocytes

VS: Vertebrae number

W: Whole body weight

List of papers

Paper I

dos Santos Schmidt, T.C., Devine, J.A., Claireaux, M., Slotte, A., Johannessen, A., Enberg, K., Óskarsson, G.J., Kennedy, J., Kurita, Y., and Kjesbu, O.S. Atlantic herring (*Clupea harengus*) compensate for environmental stressors by plastic changes in body allometrics, fecundity and egg size investment. (*manuscript*)

Paper II

dos Santos Schmidt, T.C., Slotte, A., Kennedy, J., Sundby, S., Johannessen, A., Óskarsson, G.J., Kurita, Y., Stenseth, N.C., and Kjesbu, O.S. Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well. PNAS 114(10): e1700349114.

Paper III

dos Santos Schmidt, T.C., Hay, D., Óskarsson, G.J., Slotte, A., Johannessen, A., Kjesbu, O.S. Reproductive investment and adult body growth compared among Atlantic and Pacific herring stocks (*manuscript*)

SUMMARY

Herring (*Clupea harengus* and *C. pallasii*) have an important socio-economic role worldwide and consist of diverse populations. These populations are distributed throughout both the North Atlantic and North Pacific Oceans. Herring is a capital breeder with determinate fecundity. Fecundity can easily be determined due to the clear, group-synchronous oocyte developmental growth, where all the eggs of an individual are shed at once (total spawner). For methodological reasons, therefore, this pelagic fish species is an ideal candidate to identify factors affecting reproductive investment, both within and among the rich variety of herring populations. Another reason is that each of the Atlantic herring populations display a typical spawning time, spawning location, fecundity, and egg size. Several reproductive investment studies have been conducted with herring, but a common problem observed in previous studies was the lack of standardized methodologies. The main scope of this thesis was to elucidate the differences in life history traits, focusing mainly on reproductive investment between different oceanic and local Atlantic herring populations, using a consistent methodology.

Overall, the main findings were that reproductive investment in herring populations differed particularly between spawning seasons and spatial location. Spring spawners produce large eggs in small numbers, and autumn and summer spawners produce a large number of small eggs. Fecundity, within spawning season, is size-dependent. However, within spring spawners the egg size was similar in both oceanic and local herring populations. Morphologically, three local herring (Lindås herring, Costal Skagerrak herring, and Landvik herring) were similar to the oceanic Northeast Atlantic herring populations.

Special attention was given to the Norwegian spring-spawning herring (NSSH), where changes in the life history traits (body growth, body condition, reproductive investment, and trade-offs between fecundity and egg size) over the last 20 years were correlated with biotic and abiotic factors. Over this period, temperature has increased, zooplankton biomass has decreased, particularly from 2003 to 2009, and the sum of biomass of three pelagic stocks (herring, mackerel, and blue whiting) has increased. Therefore, these parameters were considered when analyzing the changes in life history traits.

NSSH exhibited substantial physiological plasticity. This herring changed most of their life history traits to cope with dynamic biotic and abiotic changes in the Norwegian Sea. Body growth was the key trait affected, and this impacted other life history traits. Although, body growth decreased, NSSH maintained high body condition and invested more in reproduction. However, the egg production varied over the years. Interannual variation in NSSH fecundity

was demonstrated to be driven by past and current food intake. Two processes were responsible for down-regulating fecundity: apoptosis during the oogenesis, and atresia during the vitellogenic stage. Therefore, two groups of females were established: females with high fecundity ("Good-seasons females") and females with low fecundity ("Poor- and good-seasons females"). Furthermore, trade-offs between fecundity and egg size was identified. Oocytes grew faster and more in years with low fecundity compared to oocytes produced in years with high fecundity.

The findings of this thesis clarify recent processes with NSSH, but also showed a broader perspective of how herring populations differ or resemble each other. Furthermore, the findings offer new insights into future application in the other herring reproductive studies, by providing more accurate information in total egg production.

1. INTRODUCTION

Fish, in general, have an important socio-economic role in the world. The world population continues to increase, creating a greater demand for greater fishing effort. One of the greatest concerns is how to harvest these resources in a sustainable way (FAO, 2016). Biomass of several fish stocks has already significantly declined, including species within the family Clupeidae (Hutchings and Reynolds, 2004).

Atlantic herring (*Clupea harengus*) represents one of the most abundant pelagic fish species in the world, and represents a large proportion of the global marine fishery captures. Pacific herring (*C. pallasii*) is also important, but to a lesser extent commercially (FAO, 2016).

Several herring stocks in the Atlantic and Pacific Oceans collapsed at almost the same time (end of the 1960s and early 1970s) (Hourston, 1978; Hay *et al.*, 2001). The main reason for the collapse is unclear, but several factors are likely: i) the advance of new technology and engineering (e.g. the acoustic sonar, adopting the use of purse seine nets, and larger vessels) that enabled more effective search and higher catches in a shorter time (e.g. Blaxter and Hunter, 1982; Jakobsson and Stefánsson, 1999; Røttingen, 2004); ii) high exploitation of different life stages (adult and young herring as the main targets) associated with high fishing mortality (Dragesund and Ulltang, 1972; Dragesund, 1980; Toresen and Østvedt, 2000); iii) poor recruitment of the adult stocks (Dragesund *et al.*, 1980; Jakobsson, 1985); iv) changes in environmental conditions, such as temperature (Corten and van de Kamp, 1992; Toresen and Østvedt, 2000), salinity (1951 – 2004) (Astthorsson *et al.*, 2007), negative NAO (Edwards *et al.*, 2002), and El Niño events (Hay *et al.*, 2001); v) biological conditions (e.g. zooplankton availability) (Heath *et al.*, 1997; Beaugrand *et al.*, 2003; Astthorsson *et al.*, 2007); and vi) lack of effective management strategies (Røttingen, 2004). Since these stocks collapsed, significant efforts have been made to rebuild the stocks; for example, all of the Northeast Atlantic herring stocks are closely monitored and assessed annually (ICES, 2015a; ICES, 2016).

There was a high success in rebuilding the herring stock size after the collapse (Hutchings and Reynolds, 2004). However, biological and environmental impacts caused by fluctuations in stock biomass were observed (Casini *et al.*, 2006; Enberg and Heino, 2007; Heino *et al.*, 2015). A decrease in herring stock biomass may allow other fish stocks to flourish (i.e. fish replacement) (Rothschild, 1986). For instance, an inverse pattern between the biomass of Norwegian spring-spawning herring and blue whiting (*Micromesistius poutassou*) has been recorded, as well as between Baltic herring and sprat (*Sprattus sprattus*).

Any change in ecosystem, caused by fisheries, competition, and environmental change affects the top-down and bottom-up processes (Casini *et al.*, 2009; Huse *et al.*, 2012), and consequently will change the life history traits (Casini *et al.*, 2006; Enberg and Heino, 2007; Heino *et al.*, 2015).

Rothschild (1986) stated "Our concerns for fish-populations dynamics require an understanding of the entire system because the energetic exchanges associated with fish production are not restricted to one part of the ecosystem model but exist at various levels of the system". To include the commercial importance of herring, and clarify changes in life history tactics and strategies adopted by herring, in particular the Norwegian spring-spawning herring, this synthesis is divided into four main topics: 1) The background information consists of a brief description of the physical environmental conditions, bottom-up processes, and the pelagic fish fauna and its interactions in the Norwegian Sea. This is followed by a brief description of the herring populations studied, including the local Norwegian populations and the environmental features of the Norwegian fjords where they are found, as well as an overview of the life history traits of herring in general. 2) The main objectives and specifics goals of the thesis are presented. 3) A summary of the three papers produced during this study. 4) Finally, a concise discussion and conclusion relating to all the results.

1.1. Norwegian Sea (pelagic ecosystem)

The Norwegian Sea covers part of the Exclusive Economic Zone (EEZ) of Norway, Iceland and the Faroe Islands, part of the fishery zone around Jan Mayen Island, and the Fishery Protection Zone of Svalbard (Fig. 1).

1.1.1. Physical parameters

The circulation in the Norwegian Sea is represented by three water layers:
1) The upper layer is characterized by the influx of two warm and saline water masses: the Atlantic Water (AW; T > 2ºC and S > 35) and the Norwegian Coastal Water (NCW; T > 3ºC and S > 34.7), and by a cold and less saline water mass, the Arctic Water (T < 0ºC and 34.3 < S < 34.7) (Blindheim, 2004; Loeng and Drinkwater, 2007; Fig. 1). The AW drifts northwards with the Norwegian Atlantic Current (NAC) and splits into two branches; the eastern branch known as the Norwegian Atlantic Slope Current (NwASC) and the western branch, known as the Norwegian Atlantic Front Current (NwAFC) (Mork and Skagseth, 2010; Walczowski, 2013). The NwASC drifts through the Faroe-Shetland Channel and continues northwards along the Norwegian Shelf, while the NwAFC drifts across the Iceland-Faroe Ridge (Mork

and Skagseth, 2010). The AW drifts northwards and is gradually cooled and converted into the cold Arctic Water Mass, flowing back southwards driven by the East Greenland Current (Blindheim, 2004).

The NCW dominates the eastern margin of the Norwegian Shelf and is driven by the Norwegian Coastal Current (NCC). It enters in the south from the North Sea and flows towards the Barents Sea in the north-east (Blindheim, 2004). The NCC represents an extension of the Baltic Current (Blindheim and Loeng, 1981).

2) The intermediate layer is characterized by the intrusion of Arctic Intermediate Water (Blindheim, 2004).

3) The deep layer, the Norwegian Sea Deep Water (NwSDW), is represented by the influx of the Greenland Sea Deep Water and Arctic Ocean Deep Water. There is no mixing of deeper water between the Arctic and the North Atlantic waters due to the North Atlantic Ridge (Blindheim, 2004).
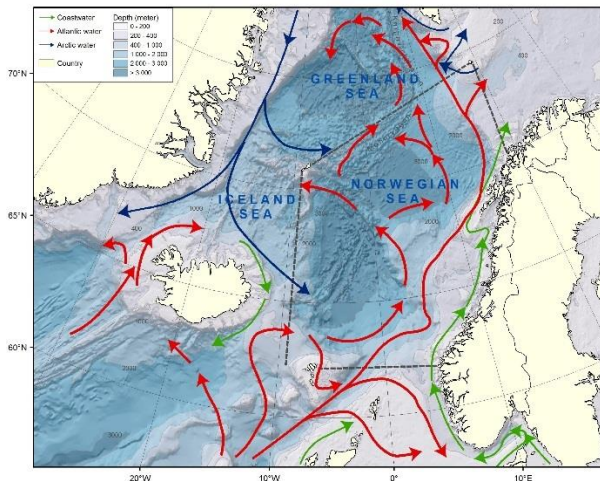
Figure 1. Norwegian Sea and adjacent areas. Arrows indicate the main circulation; red arrows represent the Atlantic water (AW), blue arrows represent the Arctic water, and green arrows represent the Coastal water (NCW). The dashed black line delimitates the Norwegian Sea area (source: Institute of Marine Research).

1.1.2. Primary and secondary production in the Norwegian Sea

Light intensity and the vertical flux of nutrients have a direct effect on the photosynthetic process (Boyd *et al*., 2014), whereas the North Atlantic Oscillation (NAO) and temperature have an indirect influence (Drinkwater *et al.*, 2003; Sundby *et al.*, 2016). The spring bloom of phytoplankton takes place close to the coast (NCW) and spreads throughout the Norwegian Sea (AW and Arctic waters) (Broms *et al.*, 2012).

The phytoplankton bloom occurs mainly in early March – April ($200 – 400$ mgCm^{-2}day^{-1}) reaching peak productivity in May ($1 – 1.5$ gCm^{-2}day^{-1}), however small blooms can also take place in autumn (Rey, 2004). The phytoplankton community in the Norwegian Sea is composed mainly of diatoms and flagellates (Rey, 2004). The species composition is related to nutrients availability. Phytoplankton is composed of diatoms when the nutrient level is high, and when the nutrients become scarce, the phytoplankton composition is replaced by

flagellates (Drinkwater *et al.*, 2003). When all nutrients consumption ends, most of the phytoplankton production is derived from regenerated production (Sundby *et al.,* 2016).

The zooplankton community is composed mainly of *Calanus* species; *Calanus finmarchicus, C. hyperboreus*, and *C. helgolandicus* represent the main zooplankton found in the Norwegian Sea, the Icelandic Sea, and the North Sea (Planque and Fromentin, 1996; Loeng and Drinkwater, 2007; Gislason and Silva, 2012). *C. finmarchicus* represents more than 90% of the total copepod biomass in the Norwegian Sea (Planque and Batten, 2000), while *C. hyperboreus* has rarely been found in the southwestern Norwegian Sea since 2003 (Kristiansen *et al.*, 2016). A few species of euphausiids or krill (e.g. *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and *T. longicaudata*) are also widely found in the Norwegian Sea (Loeng and Drinkwater, 2007); the total biomass of these krill species is 50 million tons of wet weight (Dalpadado *et al.*, 1998). In the Icelandic Sea, similar patterns have been observed. Six species of copepods represent more than 95% of the abundance and biomass, with *C. hyperboreus* and *C. finmarchicus* representing the main biomass found in this area (Gislason and Silva, 2012).

Zooplankton undertakes annual vertical migrations, i.e. overwintering in deeper waters ($\geq$ 500 m depth) and spawning in the upper layers (0 – 250 m), as well as diel vertical migrations (DVM), with zooplankton located in the upper layers at night to feed and seek refuge from visual predators, and migrating to deep waters during the day (Lambert, 1989; Liu *et al.*, 2003). DVM is not very evident during the summer, the juvenile stages are located above 40 m during both day and night, and the main concentration of advanced copepodite stages (CV and CVI) occurs below 30 m (Dale and Kaartvedt, 2000).

Overall, the zooplankton are concentrated in the western, northern, and north-eastern areas of the Norwegian Sea (60 – 70ºN) (Misund *et al.*, 1998). *Calanus* spp. overwinter in deep areas in the Norwegian Sea, around Iceland, and the western parts of Spitsbergen. Recently, a high abundance of copepodite stage V (CV) of *C. finmarchicus* was found overwintering inside Vestfjorden in northern Norway (Espinasse *et al.*, 2016).

The ascent to the surface and spawning cycle are synchronized with the phytoplankton blooms (Kaartvedt, 2000). Geographical occurrence and distribution of *C. finmarchicus* is associated with nitrate and chlorophyll-*a* concentrations (Broms and Melle, 2007). The onset of *Calanus* production is located at the Norwegian coast and spreads into the Norwegian Sea, south of Iceland, and west of Spitsbergen (Hjøllo *et al.*, 2012). *C. finmarchicus* migration towards the upper layers takes place in March; the zooplankton production starts in April (mainly in Coastal Water), with young copepodite stages (CI – CIII) being found in May, and

the bulk occurring in July (Broms and Melle, 2007; Hjøllo *et al.*, 2012). Temporal differences in zooplankton production and copepodite stages can be found in all three water masses (NCW, AW, and Arctic Water). Old copepodite (CV and CVI) stages are found in all water masses after June, with peak of CV from mid-July to mid-August (Broms and Melle, 2007). Normally, high abundance of *Calanus* spp. is found near Iceland in mid-August (Utne *et al.*, 2012b).

In the North Sea, for example, spatial and temporal segregation has been identified between *C. finmarchicus* and *C. helgolandicus* (Planque and Fromentin, 1996). *C. finmarchicus* is dominant during the spring bloom, but is replaced by *C. helgolandicus* during the autumn bloom. *C. helgolandicus* is more abundant in the Celtic Sea during the spring bloom, but migrates northwards into the North Sea during the summer. This inverse distribution in abundance is determined by the sea water temperature, i.e. *C. finmarchicus* is more abundant during the spring due to the cold water, while *C. helgolandicus* is abundant in the southern part during the spring and in the north during the autumn due to warmer water (Planque and Fromentin, 1996).

Environmental factors, such as increasing temperature, wind speed, the NAO, humidity, and AW inflow, have caused changes in zooplankton diversity, abundance, and distribution since the early-1960s (Fromentin and Planque, 1996; Planque and Fromentin, 1996; Alvarez-Fernandez *et al.*, 2012). Because of the warming, cold water copepod species (*C. finmarchicus*) in the North Sea have been replaced by warm water species (*C. helgolandicus*) (Alvarez-Fernandez *et al.*, 2012). In the Barents Sea, however, no shift in abundance has so far been observed between *C. finmarchicus* and *C. helgolandicus* due to ocean warming (Dalpadado *et al.*, 2012). However, a simulation indicated that *C. finmarchicus* will be restricted to the Barents Sea due to warm waters, whereas *C. glacialis* will disappear from the area (Slagstad *et al.*, 2011).

There has been an overall decline in zooplankton biomass in the Norwegian Sea (ICES, 2014c). A 50% drop in biomass was observed from 1958 to 1997 (Planque and Batten, 2000), and the decline was even greater from 2003 to 2009 (~ 70%) (ICES, 2014c). This drop in zooplankton biomass has been related to the intense predation by planktivorous fish (Huse *et al.*, 2012a; see below).

1.1.3. Pelagic fish stocks in the Norwegian Sea

The Norwegian Sea is the major feeding grounds of the three largest commercially important pelagic fish species in the North Atlantic: the Northeast Atlantic mackerel (NEAM;

Scomber scombrus Linnaeus, 1758), blue whiting (BW; *Micromesistius poutassou* Risso, 1827), and the Norwegian spring-spawning herring (NSSH; *Clupea harengus* Linnaeus, 1758) (Langøy *et al.*, 2012; Utne *et al.*, 2012a; Bachiller *et al.*, 2016).

1.1.3.1. Northeast Atlantic mackerel

The NEAM (hereafter referred to as mackerel) has a wide distribution and is divided into three main spawning stocks: the North Sea, the Western (Biscay to northwest of Scotland), and the Southern (Gibraltar to southern Biscay) (Iversen, 2004; Fig. 2a). The spawning stock biomass (SSB) doubled from 2.2 million tons in 2005 to 4.4 million tons in 2013; with corresponding fish landings following the same trend (ICES, 2015b; Fig. 2b).
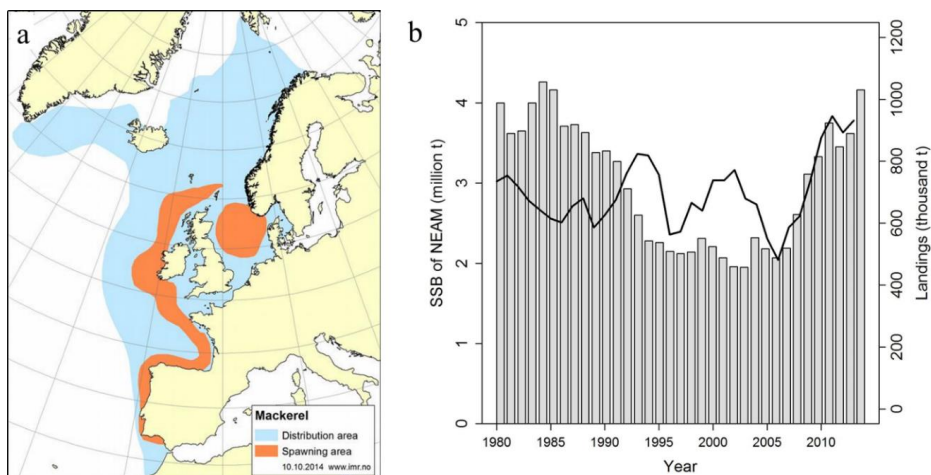
Figure 2. Mackerel distribution area (a), stock biomass and fish landing (b) from 1980 until 2014 (source: Institute of Marine Research; ICES, 2015b). (b) Bars represent the stock biomass and the solid line represents the fish landings.

The NEAM spawning season starts at the end of January and ends in mid-July (ICES, 2014d). The peak occurs mainly during the spring and early summer (May – June). Spawning takes place in three main areas: i) the southern areas from Gibraltar to Bay of Biscay, ii) the western areas of British Isles, and iii) central areas in the North Sea (Iversen, 2004; Jansen and Gislason, 2013; Fig. 2a).

Feeding migration starts after spawning. NEAM is found in the Norwegian Sea during the feeding season (June – September) (Loeng and Drinkwater, 2007; Nøttestad *et al.*, 2016b). The migration to the feeding areas is size- and temperature-dependent, i.e. large fish arrive

earlier and leave later than smaller fish (± 20 days); and also arrive earlier in warmer waters (Jansen and Gislason, 2011). During the feeding, mackerel migrates from areas in the south towards the Norwegian Sea, spreading throughout the area (Utne and Huse, 2012; ICES, 2014d). The abundance of mackerel, however, is concentrated in the central and southern areas of the Norwegian Sea, mainly associated with the AW (Utne *et al.*, 2012a; Bachiller *et al.*, 2016). NEAM has undertaken the same feeding migration pattern over many years (Nøttestad *et al.*, 2016b). However, this pattern changed in 2015, when NEAM migrated mainly west to Greenland waters (south of Iceland towards west), where they found warm temperatures and higher zooplankton concentration (Nøttestad *et al.*, 2015).

After the feeding period, mackerel leaves the feeding grounds and is distributed along the Norwegian Trench (continental shelf edge) (Jansen *et al.*, 2012). During the winter, mackerel is located in bottom waters, aggregating in large schools (Iversen, 2004).

The NEAM is an opportunistic species, but their energy intake is optimized by shifting prey preference, according to prey abundance or size selection (Pepin *et al.*, 1988). The diet of the larvae is size dependent, mainly composed of zooplankton copepods (Ware and Lambert, 1985). The adult mackerel diet consists mainly of copepods (*C. finmarchicus*, *Pseudocalanus elongatus, Oithona similis, Temora longicornis, Acartia clausi,* and juvenile *Metridia* spp.), herring larvae, Cladocera, and euphausiids (Prokopchuk and Sentyabov, 2006; Langøy *et al.*, 2012; Skaret *et al.*, 2015; Bachiller *et al.*, 2016). NEAM also demonstrate geographical and seasonal food preference. In the AW, the main prey is *C. finmarchicus* and, in the Arctic waters and the NCW, the diet is composed of appendicularians and euphausiids, respectively (Bachiller *et al.*, 2016). Mackerel in Portuguese waters preys upon euphausiids during the summer, blue whiting and decapods during the autumn, and decapods larvae during the winter (Cabral and Murta, 2002).

Mackerel is an asynchronous species (see definition at Table 4) and spawning occurs in batches (5 – 7 batches) (Morse, 1980; Murua and Saborido-Rey, 2003). Eggs are normally concentrated at the surface, mainly above the thermocline (Ware and Lambert, 1985). Mackerel produces pelagic eggs (± 1 100 – 1 300 µm) with an average relative fecundity around 1 200 eggs gram[-1] per female (Ware, 1977; ICES, 2014b). The peak egg production is driven by temperature (Jansen and Gislason, 2011), and spawning is synchronized with the peak of zooplankton production (Ware, 1977). Consequently, egg diameter decreases during the spawning season in accordance with zooplankton size. In St. Georges Bay (Nova Scotia), mackerel spawning occurs in mid-July at temperatures between 10 – 15ºC, and eggs hatch within 5 – 7 days (10 – 14ºC) (Ware, 1977; Ware and Lambert, 1985). As with the NWA

mackerel, the NEAM also arrives at the spawning grounds when they can find appropriate temperatures. Larvae and juveniles soon actively migrate to nursery areas (Trenkel *et al.*, 2014 and references therein) located around Ireland, north and west of Scotland (north of 59ºN), and the Bay of Biscay (Jansen *et al.*, 2015).

Temperatures of 8ºC have been considered to be the lowest threshold temperature for mackerel migration activity (Ware and Lambert, 1985). However, mackerel schools have been found in areas with temperatures of 6ºC (Nøttestad *et al.*, 2016b). Usually, mackerel avoids cold water conditions by swimming actively (Jansen *et al.*, 2012). The increase in distributional area of mackerel has been attributed to warming of the ocean (Astthorsson *et al.*, 2012; Nøttestad *et al.*, 2016b). Mackerel was for the first time recorded in the Svalbard area in 2013 (Berge *et al.*, 2015).

1.1.3.2. Blue whiting

BW is distributed along the Northeast Atlantic (NEA) Ocean, from the Iberian Peninsula and the Mediterranean to the Barents Sea (Fig. 3a). The BW stock is composed of two components: the southern (Bay of Biscay) and the northern (Ireland) components (ICES, 2014d). However, the two components are managed as a single stock (ICES, 2014d). The SSB peaked in 2003 at about 7 million tons, but decreased thereafter. Currently, the SSB of BW has increased to ca. 4 million tons (Fig. 3b), and fishing mortality (F) has also shown a positive trend (ICES, 2015b).

Juvenile and adult BW show different habitats and feeding preferences (Monstad, 2004; Utne *et al.*, 2012a). Adult BW conduct DVM, and are located at 100 – 200 m during the night and move to deeper waters (300 – 500 m) during the day (Bailey, 1982). Juveniles, on the other hand, are distributed in shallower waters on the continental shelf and oceanic banks (Bailey, 1982). Juveniles are normally found in the Norwegian Sea throughout the year, whereas adults undertake extensive migrations towards the Norwegian Sea for feeding (Monstad, 2004; ICES, 2015b). The feeding season occurs in late spring and summer (Langøy *et al.*, 2012). The distribution pattern at the feeding grounds depends on food availability and environmental conditions (Monstad, 1990); however, the BW is usually located in the AW and NCW at 4 – 7°C (Bachiller *et al.*, 2016). Geographical distribution of BW in the Norwegian Sea is also density-dependent, i.e. when the stock size is low the BW is located in the southern and eastern areas, but when the stock size increases, BW is distributed throughout the Norwegian Sea (Utne *et al.*, 2012a).
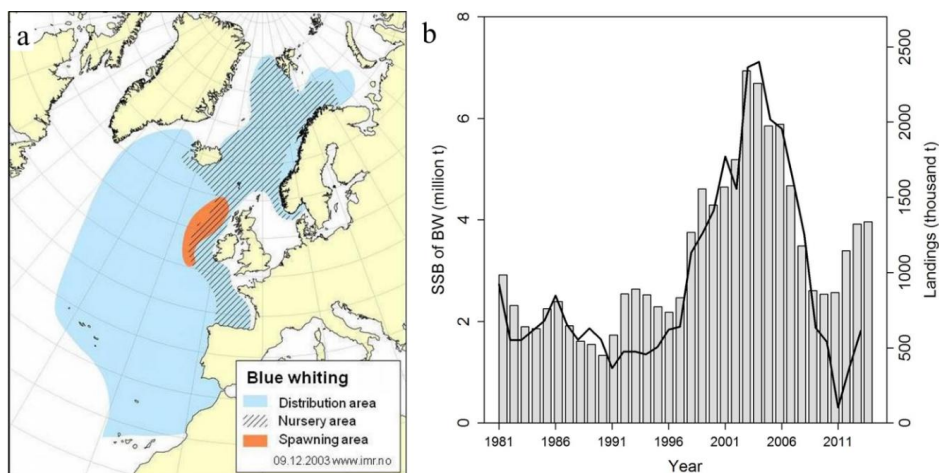
Figure 3. Blue whiting distribution area (a), stock size and landing of blue whiting (BW) (b) from 1981 to 2014 (source: Institute of Marine Research; ICES, 2015b). (b) Bars represent the stock biomass and the solid line refers to the fish landings.

The BW has an important role in the pelagic ecosystem, both as predator on zooplankton and fish larvae, and as the prey of large fish and cetaceans (Heino and Godø, 2002). The main BW prey consists of crustaceans: mainly copepods, euphausiids, and larvae of decapods (Cabral and Murta, 2002). Seasonal diet and size preferences have also been observed (Bailey, 1982; Cabral and Murta, 2002). BW larvae prey upon copepods *Oithona, Calanus, Pseudocalanus*, and *Acartia* (Bailey, 1982). Adult BW prey upon *Pasiphaea sivado* during the autumn, and *Meganyctiphanes norvegica*, during the winter. Copepods are consumed during both summer and winter (Cabral and Murta, 2002). In the Norwegian Sea, the BW diet consists of euphausiids, amphipods (*Themisto* spp.), and appendicularians (Langøy *et al.*, 2012; Bachiller *et al.*, 2016). In Portuguese waters, the main predators of BW are hake (*Merluccius merluccius*) and mackerel.

BW matures at lengths 16 – 20 cm and at ages 3 – 7 years (Pawson, 1979; Bailey, 1982). Egg diameter ranges between 990 and 1 250 µm (Bailey, 1982), and they are deposited in cold water below the thermocline, at 400 – 600 m depth (Kloppmann *et al.*, 2001). There is a vertical segregation in BW eggs and larvae; eggs are located in deeper water (< 500 m depth) while larvae are found much shallower (0 – 150 m depth) (Ådlandsvik *et al.*, 2001). Larvae are distributed along the southwestern slope of the Porcupine Bank and southern Irish shelf edge, mainly in March/April, and located in the northeast of the Porcupine Bank in May (Kloppmann *et al.*, 2001).

1.1.3.3. Norwegian spring-spawning herring

Details of this stock are described in the Herring population structure (section 1.2) as well as in the Norwegian spring-spawning herring (subsection 1.2.1.1).

1.1.4. Interspecific competition

Sympatric and allopatric species may compete for the same food resource (Wootton, 1990). As stated above, the three largest pelagic fish stocks (BW, NEAM, and NSSH) co-occur in the Norwegian Sea during the feeding season (Table 1). Currently, these three stocks sum about 13 million tons (ICES, 2015b). Competition for space (both horizontally and vertically) and niche overlap have been documented between these species (Huse *et al.*, 2012a; Bachiller *et al.*, 2016). The NSSH distribution area overlaps with young BW (Huse *et al.*, 2012b) and mackerel (Bachiller *et al.*, 2016). However, in general, NSSH and NEAM demonstrate low horizontal overlap, whereas BW shares the same horizontal area with NSSH and NEAM, but not vertically; in all the cases, some encounters take place during the feeding season (Utne and Huse, 2012; Bachiller *et al.*, 2016).

These fish stocks display spatio-temporal segregation in the Norwegian Sea. NSSH is the first to arrive in the area in a given feeding season, followed by BW, and then mackerel (Kaartvedt, 2000). Generally, NSSH and BW start feeding in the south and central areas of the Norwegian Sea, and migrate northwards in the summer, expanding their distribution in the entire Norwegian Sea. The NEAM then arrives to start feeding (Utne *et al.*, 2012b). NSSH and BW are normally found in different depth strata in Arctic waters, although NSSH can also be found in AW (Huse *et al.*, 2012b; Langøy *et al.*, 2012). The distribution of NSSH is associated with high densities of food (Huse *et al.*, 2012b; Nøttestad *et al.*, 2013), whereas BW is found in colder waters and in the presence of larger prey (Langøy *et al.*, 2012). NEAM is mainly located in warmer waters (AW and NCW; temperatures above 6ºC), regardless of food density (ICES, 2014d). The co-occurrence of these stocks in the ecosystem increased the competition for food. NSSH and NEAM share the same diet, whereas BW has a different food preference (Bachiller *et al.*, 2016).

The simultaneous decline in zooplankton biomass and intense predatory activity of NSSH, BW, and NEAM (Dalpadado *et al.*, 2000; ICES, 2015b) suggest that the Norwegian Sea has reached its carrying capacity (Huse *et al.*, 2012a). Concerns have therefore been raised about ecosystem functioning and possible changes in the life history of these fish (e.g. Research Council of Norway (NFR) project INFERNO, see Huse *et al.* (2012a)).

Table 1. Summary of annual migration time and geographical location of the pelagic fish stocks.

	NEAM	BW	NSSH
Spawning season	May - June (February - July)	January - May	February - March
Spawning area	Bay of Biscay, west of Great Britain, and east Ireland	Porcupine Bank and Bay of Biscay	Norwegian coast (63° - 70°N)
Feeding season	June - September	May - September	April - September
Feeding area	Norwegian Sea	Norwegian Sea	Norwegian Sea
Food item	copepods, Cladocera, euphausiids, and herring larvae	euphausiids, amphipods, and appendicularians	copepods, euphausiids, amphipods, and appendicularians
Overwintering area	Norwegian Trench	-	North of Vesterålen

1.2. Herring population structure

Herring belongs to the order Clupeiformes and family Clupeidae; the genus *Clupea* is composed of two species (*Clupea harengus* and *C. pallasii*) (Whitehead, 1985; Nelson, 2006). Clupeiformes are of worldwide commercial importance (FAO, 2016).

Herring are distributed in both the Atlantic (*Clupea harengus* L.) and the Pacific Oceans (*Clupea pallasii* V.) (Hay *et al.*, 2001). In the Atlantic Ocean, the eastern Atlantic herring occur from northern Bay of Biscay to southwest Greenland and eastern Spitzbergen, and the western Atlantic herring is spread from South Carolina to Labrador. In the Pacific Ocean, eastern Pacific herring are distributed from northern Baja California and San Diego to Kent Peninsula and Beaufort Sea, and western Pacific herring located from south Japan to Anadyr Bay (Whitehead, 1985).

Both herring species consist of several stocks and/or populations[1] and represent a complex group (Iles and Sinclair, 1982; Hay *et al.*, 2001). Cushing (1967) classified herring at three different levels: a) the highest level: representing the species; b) the intermediate level: representing the different spawning groups (e.g. spring spawners, autumn spawners); and c) the lowest level: representing a specific stock/population (Fig. 4). The populations are normally designated according to spawning season and geographical location (Parrish and Saville, 1965). In the NEA the major known herring populations known are the NSSH,

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[1]Hereafter, all herring will be referred to as population, however, when referring to management these populations will be named as stocks. Stocks, components, and population concepts are outlined in Langård (2013) and Eggers *et al.* (2014).

Icelandic summer-spawning herring (ISSH), North Sea autumn-spawning herring (NSAH), North Sea winter-spawning herring (NSWH), Celtic herring, Irish herring, West Scotland herring, and Baltic herring (Hay *et al.*, 2001). The Baltic herring (*Clupea harengus membras*) is usually referred to as a subspecies (Blaxter, 1985; Hay *et al.*, 2001). Although, there is little genetic difference between the Baltic and Atlantic herring, there is a phylogenetic differentiation (independent loci) between them (Lamichhaney *et al.*, 2012; Martinez Barrio *et al.*, 2016). Besides this, Atlantic and Baltic herring are more similar to each other than they are to the Pacific herring (Martinez Barrio *et al.*, 2016).

Herring populations are also divided into two different categories according to their spatial distribution: oceanic populations and local (coastal and fjord) populations (Fig. 4). Oceanic populations are large populations with oceanic migrations. Local populations represent small herring populations that are restricted to the coastline, fjords or sea lochs (Holst *et al.*, 2004). Two oceanic herring populations are known in the Norwegian Sea: NSSH and Norwegian summer-autumn spawning herring (NASH) (Husebø *et al.*, 2005; Pampoulie *et al.*, 2015; **Paper II**). The two populations are, however, assessed and managed as a single stock unit (ICES, 2015b). Several local Norwegian herring populations can be found. These populations are usually denominated by the name of the fjord they reside in (e.g. Balsfjord herring, Sognefjord herring, Trondheimfjord herring, and Lindås herring).

This thesis focuses on both oceanic and local herring populations found in the NEA (Fig. 4), with a special focus on populations found in the Norwegian Sea and along the Norwegian coast. A Pacific herring population, the British Columbia herring (BCH), and a Northwest Atlantic (NWA) herring population, the Scotia-Fundy herring (SFH), were used as contrast populations (**Paper III**). A description of each population is provided in the following subsections.
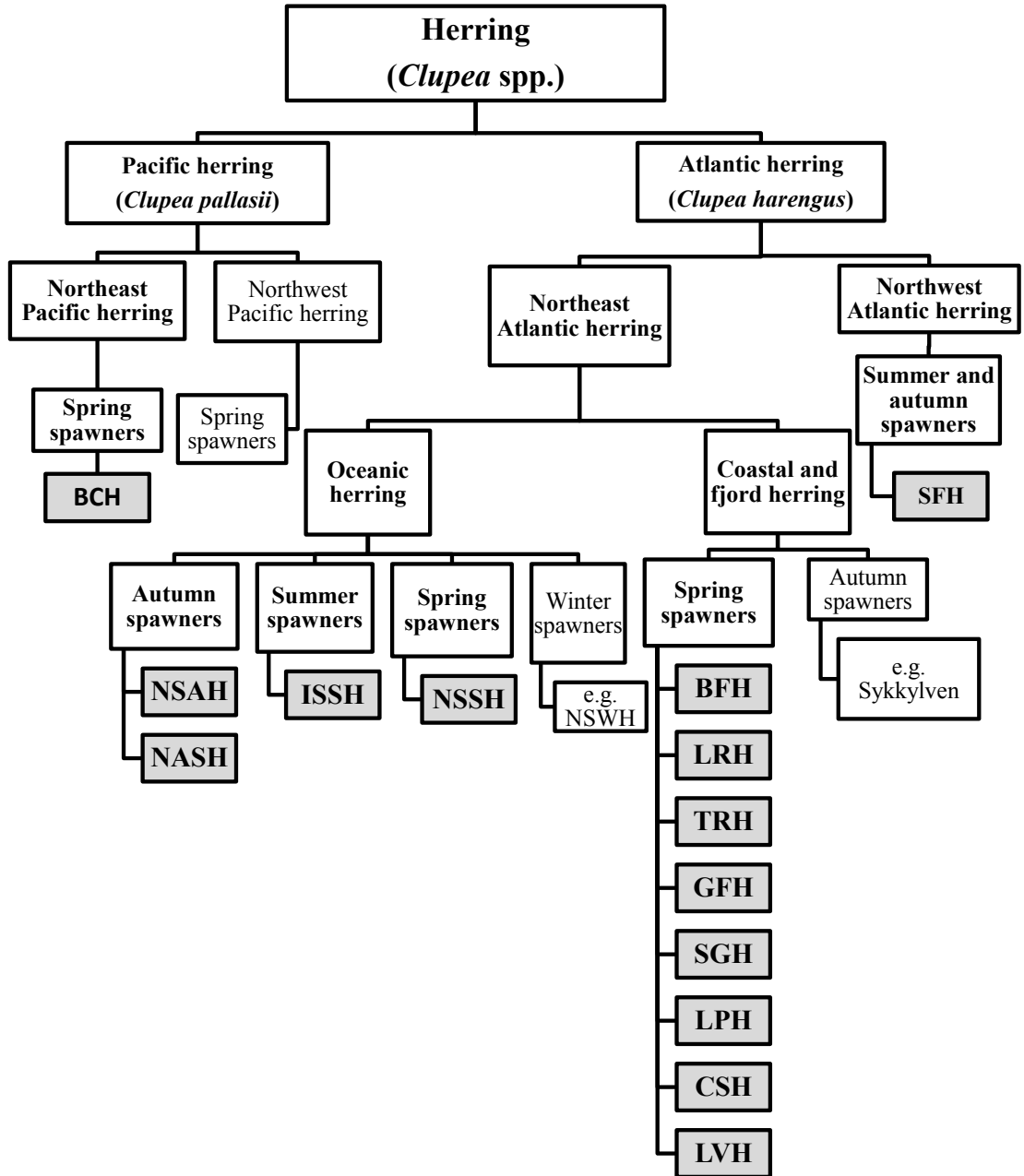
Figure 4. Classification of herring in different hierarchical levels. Herring populations targeted in this thesis are highlighted in grey.

1.2.1. Oceanic stocks

1.2.1.1. Norwegian spring-spawning herring

Among the Atlantic herring, NSSH represents one of the largest herring stocks in the world (ICES, 2015b). The stock collapsed in the late 1960s, when the stock biomass decreased from 14 million tons to 200 thousand tons (Dragesund *et al.*, 1980; Toresen and Østvedt, 2000; Fig. 5b). The first sign of stock recovery was in 1986, due to the large recruitment of the 1983 year class (Røttingen, 1990); and subsequently, at the end of the 1990s, as a result of the strong recruitment of the 1991 and 1992 year classes (Toresen and Østvedt, 2000; Sætre *et al.*, 2002). The latter year class, represents one of the most abundant NSSH year classes produced thus far (39 billion of individuals) (Toresen and Østvedt, 2000). Recently, the SSB has reached the highest biomass post-collapse (8 million tons in 1997 and 2009) in response to the high recruitment of the 1992 (in 1997) and 2004 year classes (in 2009) (ICES, 2015b). However, there has been a continuous decrease in the SSB of NSSH since then, with 5 million tons recorded in 2014 (Fig. 5b). This reduced SSB is most likely due to a weak recruitment rate and limited zooplankton availability (ICES, 2014c; ICES, 2015b).

The NSSH undertakes extensive migration annually (Fig. 5a). The distribution cycle is separated into three main phases: spawning along the Norwegian coast, feeding in the Norwegian Sea, and overwintering in Vesterålen in northern Norway (Dragesund *et al.*, 1997; Varpe *et al.*, 2005; Huse *et al.*, 2010; Fig. 5a). The distribution and migration patterns have changed as a result of the fluctuations in the stock size (Dragesund *et al.*, 1997). Three main different migration patterns have been identified: a) the pre-collapse period, which is subdivided into three periods with evident change: 1950 – 1962, 1963 – 1966, and 1967 – 1968; b) the collapse period: 1974 – 1986; and c) the post-collapse or recovery period: 1988 – 1992 (Dragesund *et al.*, 1980; Røttingen, 1990; Misund *et al.*, 1998; Fig. 6).
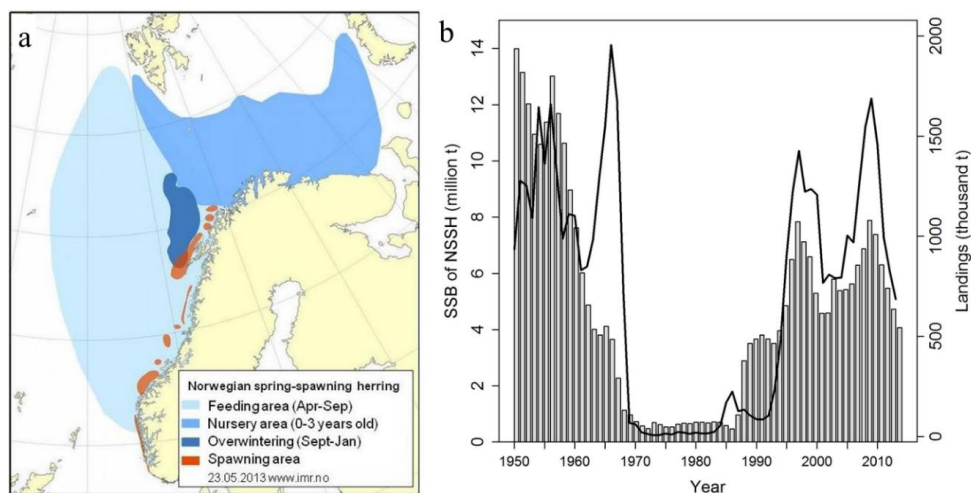
Figure 5. Norwegian spring-spawning herring (NSSH) distribution area (a), and stock size and landings from 1950 to 2014 (b) (source: Institute of Marine Research; ICES 2015b). (b) Bars represent the stock biomass and solid line, the fish landings.

a) The pre-collapse period: In 1950 – 1962, when the NSSH stock was large (~ 14 million tons), the distribution was divided into three main areas: i) the spawning ground was located from 59º to 70ºN on the Norwegian coast, mainly off Lofoten, Trøndelag, and Møre; ii) the feeding area, which was located on the border of the East Icelandic Current in the south to Jan Mayen in the north; and iii) the overwintering grounds located off east Iceland (Dragesund *et al.*, 1980; Fig. 6a).

Between 1963 – 1966, the NSSH stock divided in two components, the main component comprised of repeat spawners, and a minor component formed of recruit spawners. Thus, different distribution areas were established (Fig. 6b). The main component migrated to the same locations as previous years. The minor component, however, left the nursery areas and migrated to new feeding areas located southwest of Bear Island, and overwintered southeast of Bear Island (Dragesund *et al.*, 1980; Dragesund *et al.*, 1997; Fig. 6b).

From 1967 – 1968, the NSSH stock showed the first sign of a decline. The two components re-assembled into a single stock. The main feeding area was southwest of Bear Island and the overwintering off eastern Iceland. During this period, a reduction of the spawning grounds was recorded, located mainly in the southern area (south of Lofoten) (Misund *et al.*, 1997 and references therein). Consequently, no spawning took place at Lofoten (Dragesund *et al.*, 1980; Dragesund *et al.*, 1997; Fig. 6c).

b) The collapse period: The most dramatic change in the migration patterns was recorded between 1974 – 1986, when the distribution of the stock and migration patterns were restricted entirely to the Norwegian Coastal area (Dragesund *et al.*, 1980; Røttingen, 1990; Dragesund *et al.*, 1997; Fig. 6d). For the first time, the Norwegian fjords were used as overwintering grounds for the NSSH (Dragesund *et al.*, 1997; Huse *et al.*, 2002; Fig. 6d).

c) The post-collapse period: After the collapse, an increase in herring abundance was recorded in 1977, mainly off Trøndelag and Northern Møre (Dragesund *et al.*, 1980). In the end of the 1980s, the traditional migration route was re-established; the NSSH schools left the Norwegian coast after spawning, and migrated north- and westwards in the Norwegian Sea searching for food (Fernö *et al.*, 1998; Fig. 6e). The strong 1983 year class was responsible for re-establishing this pattern (Røttingen, 1992). In April, the NSSH was located mainly in central Norwegian Sea (Røttingen, 1990; Dragesund *et al.*, 1997; Misund *et al.*, 1997). A combination of large schools and large-sized herring allowed the migration to go even further north close to Jan Mayen and the border of the Icelandic EEZ. However, young herring were found in coastal areas, west of Lofoten during the feeding period (Misund *et al.*, 1998). The NSSH migrated north and northeast, overwintering in limited areas within Vestfjorden, Ofotfjorden, and Tysfjorden (September – January) (Røttingen, 1990; Dragesund *et al.*, 1997; Misund *et al.*, 1997; Fig. 6e). The NSSH spawning occurred from Lofoten (69°N) to Lista (58°N), within five main areas: Lofoten, Træna-Haltenbanken, Møre, Sogn-Hordaland, and Rogaland (Slotte, 1999b), with Møre being the main spawning ground (62 – 63.5ºN) (Slotte *et al.*, 2000). Although, there is still some spawning at Møre, it has recently been observed that most of the stock spawn from 63°N up to 70°N (Vikebø *et al.*, 2010). NSSH has also recently established new overwintering areas located north of Vesterålen (Northern Norway) (Huse *et al.*, 2010; Fig 6f).

DVM is also observed in NSSH in all seasons (Misund *et al.*, 1997; Huse and Korneliussen, 2000). Herring generally remain in deep waters during the day and in shallow waters at night (Blaxter, 1985). However, the depth stratum differs depending on the time of the year (Nøttestad *et al.* 2004).
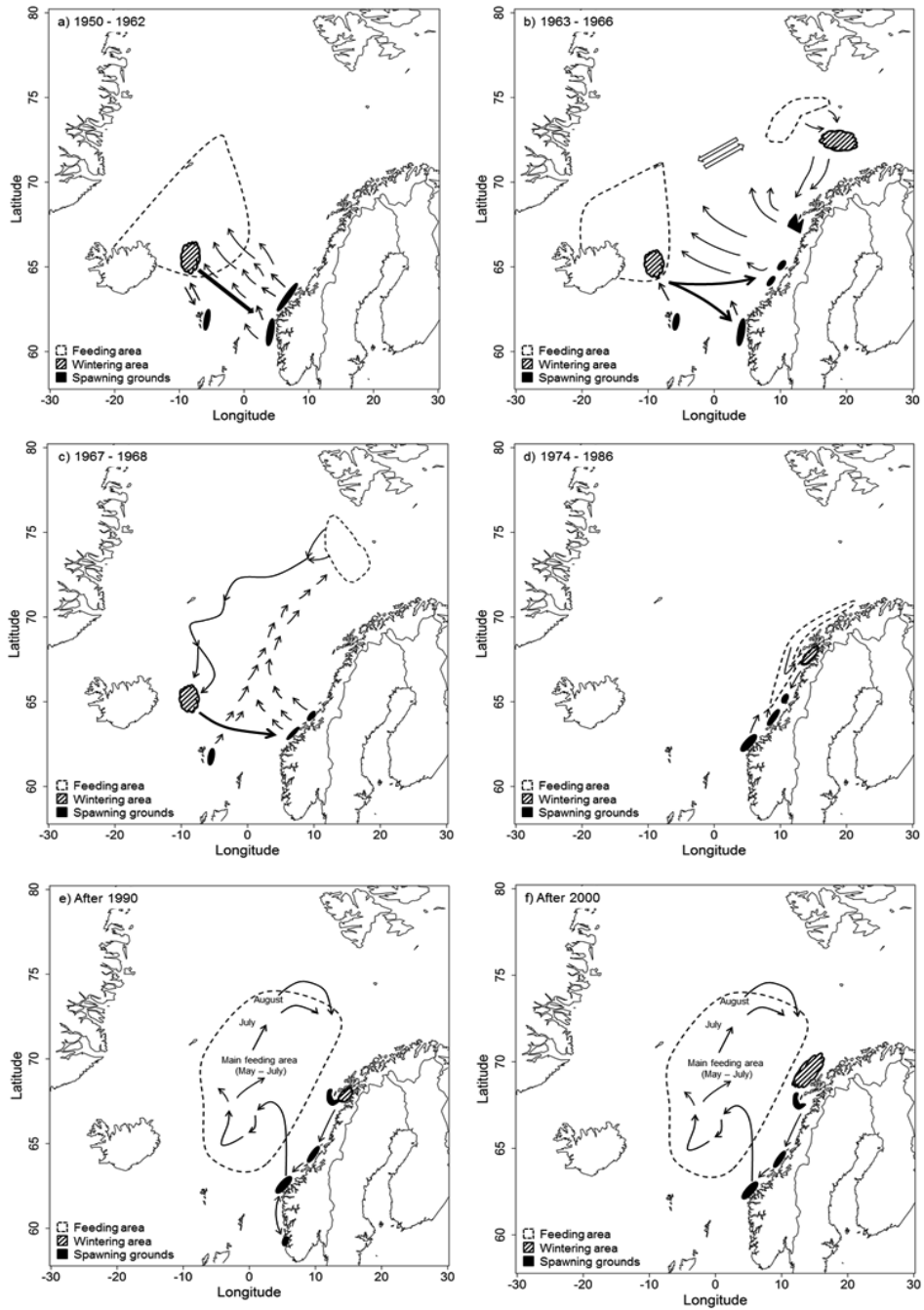
Figure 6. Norwegian spring-spawning herring distribution pattern pre-collapse (a-c), during the collapse (d) and post-collapse (e and f) (maps redrawn and modified from Dragesund *et al.*, 1997; Kvamme *et al.*, 2003; Huse *et al.*, 2010).

Food preferences usually changes throughout the fish life stages (Wootton, 1990). The NSSH larvae diet is composed of copepod nauplii, calanoid copepodites, and lamellibranchs (Gamble *et al.*, 1985). Adult NSSH feed mainly on the copepods *C. finmarchicus*, *C. hyperboreus,* and *Pareuchaeta norvegica*, but also appendicularians, amphipods, and euphausiids (Prokopchuk and Sentyabov, 2006; Langøy *et al.*, 2012; Bachiller *et al.*, 2016). *Calanus* is the main food item in May, and amphipods and euphausiids in July (Bachiller *et al.*, 2016). Active feeding occurs at 300 – 400 m depth during daytime and at the surface at night (Misund *et al.*, 1997). The feeding season is essential to support the extensive migrations, metabolism, and gonadal development (Slotte, 1999a; Holst *et al.*, 2004; Kennedy *et al.*, 2011). NSSH has a long reproductive cycle, starting in May (Kurita *et al.* 2003), when day length reaches approximately 16 hours (McPherson and Kjesbu, 2012). Spawning occurrs in February-March (Slotte *et al.*, 2000; Fig. 8). The NSSH spawning grounds are associated with retention areas (Sætre *et al.*, 2002). NSSH is characterized by homing to the spawning location, i.e. individuals return to the same areas every year (McQuinn, 1997; Fernö *et al.*, 1998). However, the spawning distribution is size and condition dependent: large fish or fish in better condition migrate further than smaller fish or fish in bad condition (Slotte, 1999b), thus, allowing them to explore different spawning grounds.

The NSSH spawn their demersal eggs (cf. 'herring reproduction') at depths between 20 – 250 m (Sætre *et al.*, 2002), where the larvae hatch between mid-March and the end of April (Gamble *et al.*, 1985; Fossum and Moksness, 1993). The NSSH has three main nursery areas: i) the Barents Sea, ii) the Norwegian fjords, and iii) the southern and eastern parts of the Norwegian Sea. The young herring stays in these areas until they are mature (Parrish and Saville, 1965). The Barents Sea represents the main nursery area, however, some NSSH larvae may end up in the fjords (Holst *et al.*, 2004). Larval drift northwards to the nursery areas takes place with the NCC (Dragesund *et al.*, 1980; Røttingen, 1990; Fossum and Moksness, 1993). This migration is density-dependent; abundant year classes tend to be distributed in the Barents Sea, whereas less abundant year classes are more restricted inside the fjords (Toresen, 1990). In early autumn, the 0-group herring, located in the entrance of the Norwegian fjords, migrate further into these areas, whereas the 0-group herring in the Barents Sea, aggregate between the cold and warm water masses (Dragesund *et al.*, 1980). Herring in the Barents Sea nursery area therefore grow slower compared to herring in the southern local fjords (Dragesund *et al.*, 1980). NSSH matures at ages 4 – 7 years and around 30 cm (Beverton *et al.*, 2004; Engelhard and Heino, 2004), and then migrates southwards into the

Norwegian Sea to congregate with the adult schools (Dragesund *et al.*, 1980; Huse *et al.*, 2002). Some NSSH, however, may remain in the fjord (Huse *et al.*, 2002).

1.2.1.2. North Sea herring

North Sea herring (NSH) is divided in three components: the northern (Orkney-Shetland herring), the central (Bank herring), and the southern (Downs herring) North Sea herring (Haegele and Schweigert, 1985; Jakobsson, 1985; Fig. 7a). The first two components are autumn spawners, and the latter is a winter spawner (Corten, 2001; van Damme *et al.*, 2009). All components are managed and assessed as a single stock (Simmonds, 2007; ICES, 2015a). However, before 1970, these components were assessed separately (Jakobsson, 1985). The NSH stock suffered two collapses, one in the late 1960s and then in the mid-1990s (Hay *et al.*, 2001). The SSB of NSH ranged from 4 million tons in the late 1940s to less than 50 000 tons in the late 1970s. The collapse was caused mainly by overexploitation (high fishing mortality) (Edwards *et al.*, 2002; Simmonds, 2007 and references therein; ICES, 2014a). Currently, the SSB is around 2 million tons (ICES, 2015a; Fig. 7b).
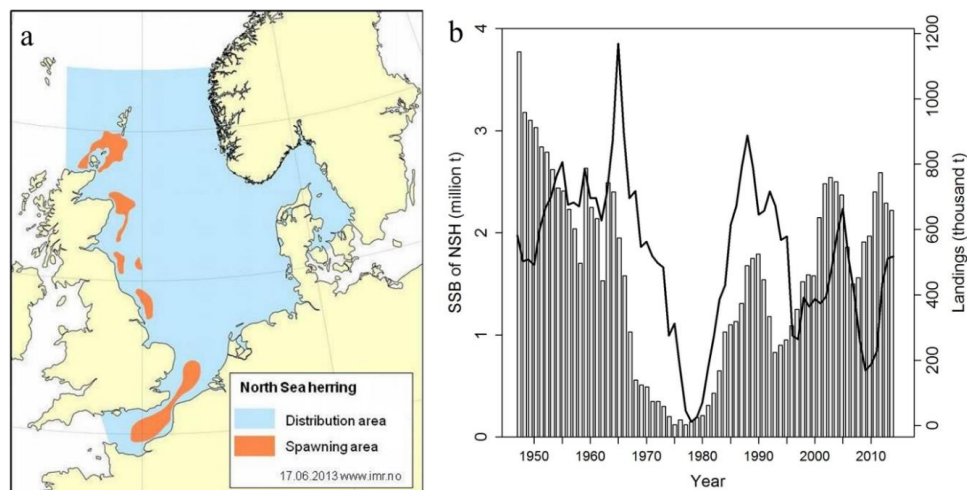
Figure 7. North Sea herring (NSH) distribution area (a), and stock size and landings from 1947 to 2014 (b) (source: Institute of Marine Research; ICES, 2013; ICES, 2015a). (b) Bars represent the stock biomass and the solid line refers to the fish landings.

The NSH larger than 25 cm are classified as repeat spawners (ICES, 2015a). NSH displays a short gonadal development cycle (Fig. 8). The onset of maturation begins in April-

May (van Damme *et al.*, 2009), more precisely after the spring equinox (McPherson and Kjesbu, 2012). Spawning occurs in August-September for autumn spawners (NSAH) (Fig. 8) and in December for winter spawners (NSWH) (Corten, 2001; van Damme *et al.*, 2009). Addressing NSWH is not within the scope of this thesis and will only be mentioned occasionally.

Spawning grounds are located in four main areas: Orkney/Shetland, Buchan, Banks, and Downs (Nash *et al.*, 2009). These areas are used by different components during various spawning seasons. Orkney/Shetland, Buchan, and Banks areas are dominated by autumn spawners, while Downs is used mainly by winter spawners (Heath, 1993; Heath *et al.*, 1997 and reference therein; Corten, 2001). After spawning, the Northern NSH migrates to the Norwegian Trench for overwintering. In spring, the NSH moves directly to the feeding grounds; active feeding takes place from April to July (Fig. 8) in different locations near the Norwegian Trench and Shetland area (Corten, 2001). These autumn components mix during the feeding season, but have distinct spawning grounds (Cushing, 1967; Hay *et al.*, 2001). Corten (2001) associated northern migrations within the North Sea area with high spring and winter temperatures and low *Calanus* abundance, and claimed that any increase in seawater temperature may accelerate gonadal development and spawning. Therefore, migrating to northern areas could be a good solution to adjust the onset of maturation to the correct period; and to ensure that all stages are synchronized with the required environmental conditions. The migration northwards can also be related to foraging (mostly driven by the presence and abundance of *Calanus* spp.). This migration pattern, however, only takes place when there is a large SSB, consisting only of older fish (Corten, 2001). Southern herring population (NSWH) feeds in the central and northern area of the North Sea, overwinters in the southern parts of the North Sea, and spawns in the English Channel, during December/January (Corten, 2001). The adult diet is composed of copepods, amphipods, and euphausiids. However, fish eggs might also be preyed upon in the absence of other typical food items (e.g. copepods) (Segers *et al.*, 2007).

NSH larvae are distributed in the North Sea, but in different areas of concentration. In general, the larvae are concentrated near the coastline, between 56º and 57ºN (Lusseau *et al.*, 2014). Herring larvae hatched (August-September) off the Shetlands and at the Buchan spawning area disperse to the northeast areas (Skagerrak), while larvae hatched at the Banks (October-December) and Downs (December-January) disperse to the central and southern parts of the North Sea, respectively (Heath *et al.*, 1997). The nursery areas of the NSH are located in shelf areas in the east of North Sea (e.g. Skagerrak, German Bight, and inlets of the

Dutch Wadden Sea) (Corten, 2013). Larvae drift to the nursery areas with the inflow of AW and appear on these grounds between January-March (Johannessen and Mokness, 1991; Corten, 2013). The diet of NSH larvae consist of copepod nauplii, cyclopoid *Oithona*, and calanoid copepods (Lusseau *et al.*, 2014).

Annual reproductive cycle of the three studied oceanic Atlantic herring populations
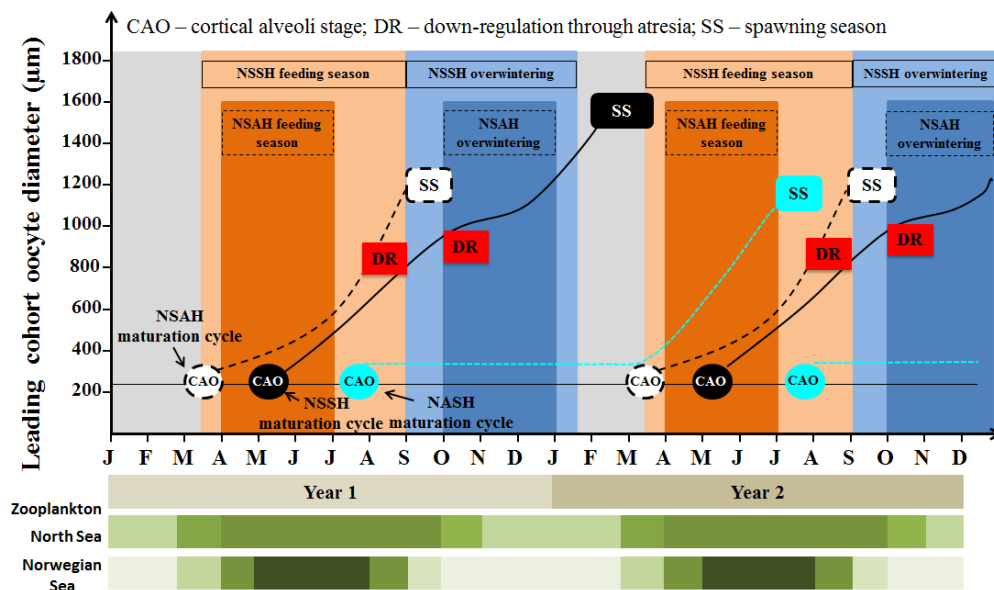
Figure 8. Schematic representation of the annual reproductive cycle of NSSH, NSAH, and NASH taking into consideration the development of leading cohort oocyte diameter (from cortical alveoli (CAO) stage until spawning (SS)). The timing of the feeding season and overwintering for NSSH and NSAH are shown; for NASH we assume the same feeding and overwintering periods as NSSH (Husebø *et al.*, 2005). Reproductive cycle information was obtained from Corten (2001); Kurita *et al.* (2003); McPherson and Kjesbu (2012); Slotte *et al.* (2000); Slotte *et al.* (2016); and van Damme *et al.* (2009). The oocyte development curve for each population is based on the results found in **Paper II** and additional information found in Slotte *et al.* (2016). The annual zooplankton production in both the North Sea and the Norwegian Sea is also demonstrated (green bars) (Sundby *et al.*, 2016).

1.2.1.3. Norwegian summer-autumn spawning herring

A relatively small herring population of summer-autumn spawners has also been found in the northern part of Norway. Limited information is available for this population. The SSB

is estimated to be around 200 000 tons (Aril Slotte *pers com*). As previously mentioned, this stock is assessed jointly with NSSH (ICES, 2015b).

The NASH was first studied in the last decade (Husebø *et al.*, 2005). More recently, the population was found to be undistinguishable from NSSH genetically, or by other means such as otolith shape and size (Libungan *et al.*, 2015; Pampoulie *et al.*, 2015; **Paper II**). Generally, NASH differs from NSSH by a slower daily otolith growth and different maturity oogive (Husebø *et al.*, 2005). In adults, total length, body weight, and therefore growth features are similar to NSSH (**Paper II**). Husebø *et al.* (2005) suggested that the population has similar ecological patterns as NSSH (e.g. same feeding, overwintering, spawning, and nursery areas), although the NASH spawning ground is exclusively located around the Lofoten area (Pampoulie *et al.* 2015). See discussion for further details (section 4.2).

1.2.1.4. Icelandic summer-spawning herring

Morphological and reproductive data of Icelandic summer-spawning herring (ISSH) (Óskarsson and Taggart, 2006) were included in **Paper III**. Although, this population is not a focus of this thesis, a brief description is provided.

ISSH belonged to the ancient group known as "Atlantic Scandinavian herring", together with NSSH and the commercially extinct Icelandic spring-spawning herring. Following the collapse of the stock, the latter component did not recover and is thus commercially extinct (Jakobsson *et al.*, 1969; Myers *et al.*, 1995). The SSB of ISSH, currently, sum ~ 350 thousand tons (ICES, 2016b; Fig. 9b).

ISSH annually migrates between the feeding, overwintering, and spawning grounds. The feeding grounds are located west and east of Iceland. Recruit and repeat spawners use different overwintering areas. Recruit spawners overwinter off southwest and repeat spawners off east Iceland. Spawning takes place south and southeast of Iceland, between Snæfellsnes and Stokksnes (Jakobsson and Stefánsson, 1999; Óskarsson and Taggart, 2009; Fig. 9a). Active feeding of ISSH occurs in May and June, then restart again in mid-August after spawning, that takes place between July and August (Jakobsson *et al.*, 1969; Óskarsson and Taggart, 2006). Spawning can be accelerated or postponed by about 10 days depending on water temperature differences. Repeat spawners (total length (TL) ≥ 30 cm) spawn before recruit spawners (TL < 30 cm) (Óskarsson and Taggart, 2009).
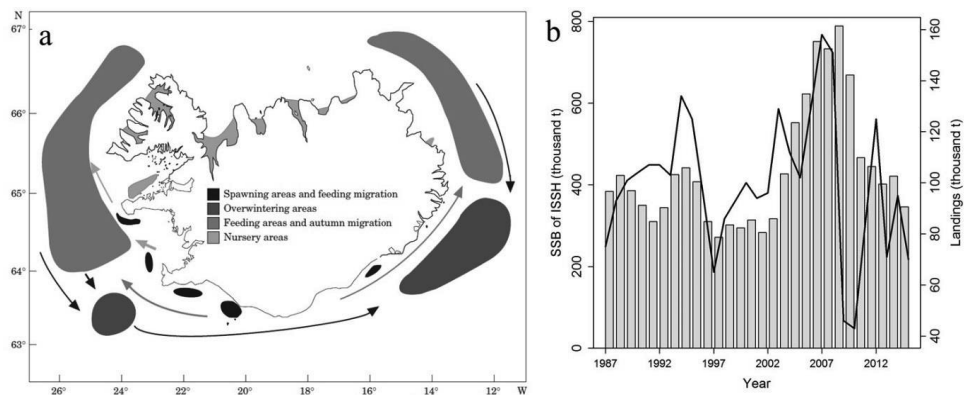
Figure 9. ISSH distribution area (a), stock size and landings of ISSH (b) from 1987 to 2015 (source: Jakobsson and Stefánsson, 1999; ICES, 2016b). (b) Bars represent the stock biomass and the solid line refers to the fish landings.

ISSH has a high growth rate, large body size (25 – 39 cm), and produces several, but small eggs (Jakobsson *et al.,* 1969; Óskarsson and Taggart, 2006; **Paper III**). ISSH has been shown to be one of the most fecund herring populations covered (**Paper III**). The gonadal maturation is short; with a resting stage of about seven months (mid-August to mid-March). Vitellogenesis takes place during the next three months, then oocytes quickly hydrate to be spawned in July-August (Jakobsson, 1969).

1.2.1.5. Scotia-Fundy summer-autumn spawning herring

Scotia-Fundy herring (SFH) is considered in this study (**Paper III**), and so, a brief description is provided. This herring populations is located in the 4VWX management area (Canada) (Power *et al.*, 2011).

SFH matures at age 3, and between 25 and 28 cm in length (Sinclair *et al.*, 1982). This herring produces a large number of small eggs; an average of 465 eggs per body gram has been reported for sexually mature females (TL: 27 – 37 cm) (Óskarsson, 2005).

Spawning takes place between summer (day of year 200) and autumn (day of year 280), mainly at German Bank, Trinity Ledge, and Scots Bay (Óskarsson, 2005; Power *et al.*, 2011).

1.2.2. Coastal and fjord stocks

Coastal and fjord herring stocks, known as local herring populations, exhibit genetically (Jørstad *et al.*, 1991; Jørstad *et al.*, 1994; Pampoulie *et al.*, 2015) and morphometrically

distinct characteristics (e.g. Lie *et al.*, 1978; Eggers *et al.*, 2014; Johannessen *et al.*, 2014; Libungan *et al.*, 2015).

The local populations, such as Landvik herring, Lindås herring, Trondheimfjord herring, and Lusterfjord herring, are genetically different from the oceanic populations. The Landvik herring population is genetically the most distinct outlier (Pampoulie *et al.*, 2015). Balsfjord herring and Lake Rossfjord herring, on the other hand, have been genetically linked to Pacific herring (Jørstad and Pedersen, 1986; Jørstad *et al.*, 1994).

The main morphometric differences of local herring compared to oceanic herring are total length, number of vertebrae (VS) (Lie *et al.*, 1978; Johannessen *et al.*, 2014), otolith shape (Eggers *et al.*, 2014; Libungan *et al.*, 2015), and differences in reproductive investment (Silva *et al.*, 2013). Like NSSH, some local populations also have well defined migration patterns to spawning, feeding, and overwintering areas inside the fjord (Lie *et al.*, 1978).

Norwegian fjords vary in topography, climate, and dynamics (Svendsen, 1995). The fjords can be open or closed systems (Kaartvedt, 1993; Bucklin *et al.*, 2000). In fjords with no or weakly developed sills, zooplankton drift into and out of the system (Bucklin *et al.,* 2000). Secondary production inside these fjords, therefore depends on advected or resident zooplankton species (Kaartvedt, 1993). Fjords also represent nursery grounds for several fish species, and many fish species spend their entire life cycle inside these fjords.

The total number of local herring populations is unknown, but several local Norwegian populations have been studied in recent years (e.g. Sørensen, 2012; Langård, 2013; Silva *et al.*, 2013; Eggers *et al.*, 2014). The local herring population studied in this thesis (**Paper III**) are: a) Balsfjord herring (BFH), b) Lake Rossfjord herring (LRH), c) Trondheimsfjord herring (TRH), d) Gloppenfjord herring (GLH), e) Sognefjord herring (SGH), f) Lindåspollene herring (LPH), g) Coastal Skagerrak herring (CSH), and h) Landvik herring (LVH). Most of these local populations have no commercial value, but they have a recreational fishery status. A brief description of these local populations and their respective areas is given below.
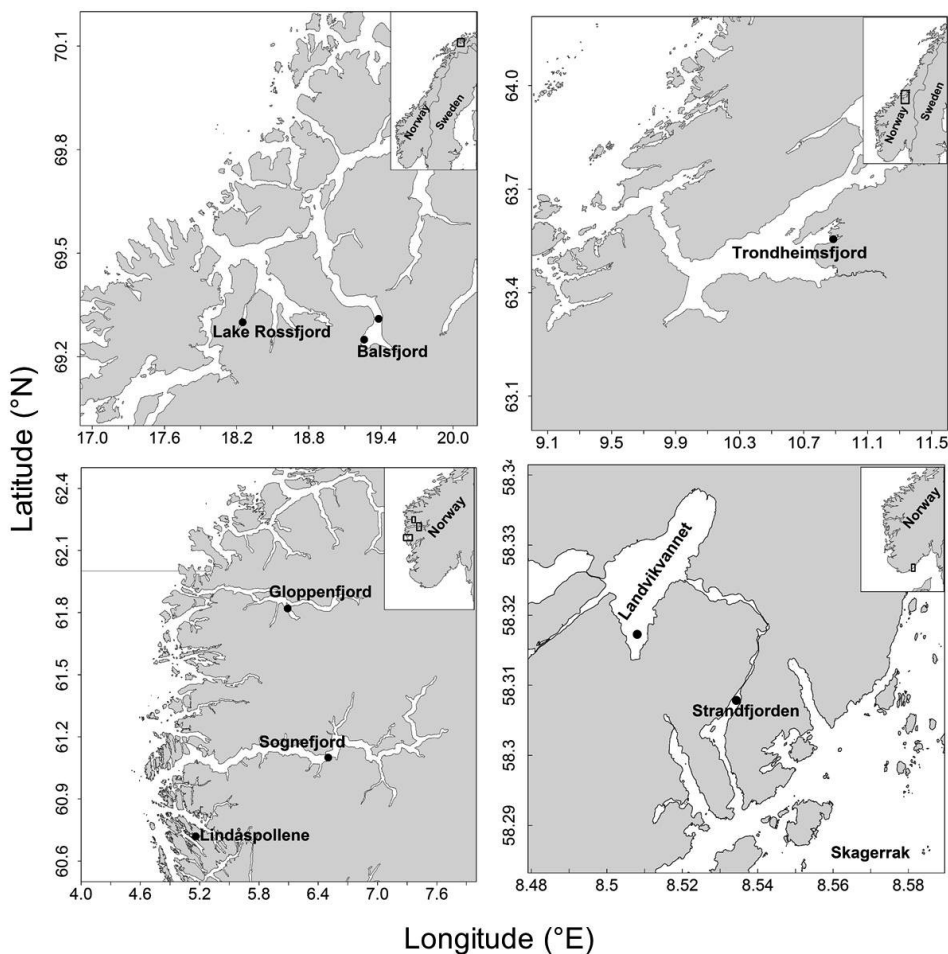
Figure 10. Study areas along the Norwegian coast. Black circles refer to herring sampling location in each fjord.

1.2.2.1. Balsfjord herring

a) Balsfjord system

Balsfjord, located in northern Norway close to Tromsø (Fig. 10), is a shallow fjord (maximum depth 195 m and sill depth 30 m) (Barthel, 1995) and is one of the coldest fjords in Norway. The water temperature ranges annually from 1 to 8ºC and salinity between 32 and 34 psu (Eilertsen *et al.*, 1981; Hegseth *et al.*, 1995; Eilertsen and Skarðhamar, 2006). Seasonal vertical stratification takes place in Balsfjord (Mankettikkara, 2013). This stratification occurs during spring and summer because of the run-off from several small rivers and snow melt

(Eilertsen and Skarðhamar, 2006), where the surface salinity reaches an average of 28 psu (Eilertsen *et al.*, 1981; Mankettikkara, 2013). The fjord circulation is divided into two layers: shallow layer (0 – 70 m) and deep layer (70 – 180 m) (Hegseth *et al.*, 1995). There is regular water circulation and oxygen concentration is high (Eilertsen *et al.*, 1981). Water exchange between the fjord and the coastal water is limited by the sills surrounding the fjord (Mankettikkara, 2013), but part of the water is renewed by the inflow of the AW during the spring (Barthel, 1995). In general, Balsfjord is characterized as a narrow fjord with moderate runoff (Svendsen, 1995).

The phytoplankton bloom starts in March-April (Vahl, 1980), the annual primary production being ca 110 gCm^{-2} (Eilertsen and Taasen, 1984). Small zooplankton are the main group in the Balsfjord system (Barthel, 1995). Three species of krill occur in the system *M. norvegica*, *Thysanoessa inermis*, and *Thysanoessa raschii* (Sargent and Falk-Petersen, 1981), together with copepods that make up the most of the biomass. The most common copepod species are *Pseudocalanus* spp., *Microclines pusillus, C. finmarchicus, Oithona* spp., *Acartia longiremis,* and *M. longa*. As expected, seasonal and spatial differences in zooplankton composition can also be found in the area (Barthel, 1995).

b) Balsfjord herring

BFH is considered to be the most distinct local herring population (Jørstad and Pedersen, 1986) in Norway. The population is more genetically similar to Pacific herring than to Atlantic herring (Jørstad *et al.*, 1994); Pacific herring migrated towards the AW during the early postglacial age (Laakkonen *et al.*, 2013; Laakkonen *et al.*, 2015). BFH is distinguished from the NSSH by two lactate dehydrogenase (LDH) loci and a glucosephosphate isomerase (GPI-2) locus (Jørstad and Pedersen, 1986; Jørstad *et al.*, 1994). Laakkonen *et al.* (2013) claimed that BFH "derived from a single surviving haplotype lineage". BFH is also distinct from other Atlantic herring population by the otolith shape (Libungan *et al.*, 2015).

Morphologically, BFH have a low vertebrae count (VS; 52 – 55) and adult body length ranges from 24 to 30 cm (Jørstad and Pedersen, 1986), with an asymptotic length (L$_\infty$) of 32 cm (Jørstad and Pedersen, 1986). However, recently, L$_\infty$ was recorded at 28.5 cm and average VS of 55 (Mikkelsen *et al.*, 2016; **Paper III**). Recruit spawners are typically 4 years (TL ~ 22 cm), and repeat spawners are between 4 and 6 years (TL ~ 25 cm; Mikkelsen *et al.*, 2016). BFH produces on average 14 000 eggs around 1 200 μm (**Paper III**). Spawning occurs in early April in the shallow inner parts of the fjord (Holmenes), and last for just a few days (Kjørsvik *et al.*, 1990). Eggs are laid on the vegetation, *Fucus* sp. and *Ascophyllum* sp., in a single-thick layer (Kjørsvik *et al.*, 1990; Jørstad *et al.*, 1994).

1.2.2.2. Lake Rossfjord herring

In the scientific literature, only one publication describes the underlying environmental features, as well as morphology and ecological characteristics of this herring population (Hognestad, 1994). Recent studies of the biology and reproduction of LRH are presented in Mikkelsen *et al.* (2016) and **Paper III**.

a) Lake Rossfjord system

Lake Rossfjord (Fig. 10) is composed of superficial layer of freshwater with a constant runoff and anoxic water below 10 – 15 m. The lake is 60 m deep, 12 km long, and 1 km wide. Surface temperature ranges from below 0ºC (ice cover) to 18 – 20ºC (summer). The salinity increases with depth and ranges from 16 (10 – 15 m) to 22 – 24 psu (20 m depth). The lake bottom consists of gravel, red algae, and big rocks. The lake is covered with ice from November to May (Hognestad, 1994). The herring is the most abundant fish species inside the lake, but other species, such as salmon (*Salmo salar*), cod (*Gadus morhua*), three-spined stickleback (*Gasterosteus aculeatus*), saithe (*Pollachius virens*), flounder (*Pleuronectes flesus*), haddock (*Melanogrammus aeglefinus*), eels (*Anguilla anguilla*), and perch (*Perca fluviatilis*) are also present (Hognestad, 1994).

b) Lake Rossfjord herring

The LRH have a small body size (TL 20 – 24 cm), a fast growth rate, reduced number of vertebrae (53.1 – 54.8), and a short life span (4 – 5 years) (Hognestad 1994). Specimens caught in 2014 ranged from 16.5 – 20.5 cm, with an average VS of 54.2, and L_∞ was 21 cm (Mikkelsen *et al.*, 2016; **Paper III**). LRH matures at age 3, and produces small numbers of large eggs (4 000 – 7 000; 800 – 1 300 µm, respectively) (Hognestad, 1994). Recently, similar average fecundity was estimated (7 500 eggs at 1 300 µm) (**Paper III**). Spawning occurs in May-June, after the ice melts, in five different areas of the lake (Steinora, Bjørnora, Tårnelv, Mølnelv, and Lindberg). This population does not form schools and the diet is composed of marine crustaceans and freshwater insect larvae (Hognestad, 1994).

1.2.2.3. Trondheimsfjord herring

a) Trondheimsfjord system

Trondheimsfjorden is located in mid-Norway (Fig. 10), and represents a deep-water fjord (maximum 500 m depth). There are several narrow channels and shallow inlets connected to the main fjord (Hjort and Dahl, 1900). The temperature at the surface (0 – 10 m) ranges from 3 – 15°C throughout the year (Öztürk *et al.*, 2002). The bottom is composed of

mud and rock (Hjort and Dahl, 1900). Cod, saithe, pollock, haddock, hake, and crabs are the main resources found in the fjord (Tiller *et al.*, 2015).

b) Trondheimsfjord herring

Adults TRH reach from 24 to 29 cm in TL, have VS around 56.4, and matures at 17 cm length and age 2 – 3 (Sørensen, 2012; **Paper II**). TRH is a stationary population, with slow growth rate, low condition prior to spawning (Sørensen, 2012; Silva *et al.*, 2013), and produces on average 23 000 eggs per female (**Paper III**).

The main known spawning areas are Åsenfjorden, Stjørdalsfjorden, around Tautra island, outside Levanger, in Hjellebotn, near Steinkjer, and in Verrasundet, a long and narrow branch of the main fjord (Sørensen, 2012 and reference therein). Prespawning herring conduct DVM, schools are located at a maximum depth of 10 m during the day and deeper than 10 m during the night; overwintering takes place at 20 m depth (Skaret *et al.*, 2006).

1.2.2.4. Gloppenfjord herring

a) Gloppenfjord system

Gloppenfjord represents one branch of the Nordfjord (Western Norway) (Fig. 10), which is a long fjord (110 km).

b) Gloppenfjord herring

Limited information is available on the GLH (Libungan et al., 2015; **Paper III**). Adult GLH have a small body size (24 – 32 cm) and VS around 56.1 (**Paper III**). The otolith shape is similar to the Lusterfjord herring (located at Sognefjord) (Libungan *et al.,* 2015). A mean of 26 000 eggs at 1 150 µm are produced by GFH (**Paper III**).

1.2.2.5. Sognefjord herring

a) Sognefjorden system

Sognefjorden is located Western Norway (Fig. 10). It is the deepest (~1 300 m) and longest (205 km) fjord in Norway (Bagøien *et al.*, 2001; Manzetti and Stenersen, 2010). Lusterfjord is the longest branch of the Sognefjord system (Manzetti and Stenersen, 2010). Temperature and salinity fluctuate in the upper 100 m, but become uniform below 100 m (around 7 – 8ºC and 34 – 35 psu, respectively) (Bagøien *et al.*, 2001). The Sognefjord fauna are composed of *C. finmarchicus* and *C. helgolandicus* (Bucklin *et al.*, 2000); fish species like herring, sprat (*Sprattus sprattus*), mackerel (mainly in autumn), cod, pollock (*Pollachius pollachius*), halibut (*Hippoglossus* sp.), and haddock (Manzetti and Stenersen, 2010).

b) Sognefjord herring

Adult SGH have a small body size (19.5 – 28.5 cm) and a low VS (56.3). Females produce on average 19 000 eggs at 1 100 µm per individual (**Paper III**). In the Lusterfjord, branch of the Sognefjord, there is a herring population known as Lusterfjord herring (Aasen, 1952). This population is also characterized by a short life span, small size (± 21 cm), slow growth rate and low number of vertebrae (56.25). Spawning occurs mainly in April (March-May) at 5 – 15 m depth (Aasen, 1952).

1.2.2.6. Lindås herring

a) Lindåspollene system

Lindåspollene (South-western Norway) (Fig. 10) is made up by three basins (Straumsosen, Spjeldnesosen, and Fjellangervågen) connected to the outside fjord by narrow sills. The depth of these basins ranges from 60 to 90 m (Dahl *et al.*, 1973). Sea water temperature varies from 5 to 7ºC (January – March), and salinity 30 – 32 psu (Langård *et al.*, 2014). Oxygen concentration is 2.5 ml/l during spring (Aksnes and Magnesen, 1983).

The secondary productivity (zooplankton biomass) is low during the winter, around 0.1 – 0.2 ml/m^3 (Dahl *et al.*, 1973). The main zooplankton species are *P. elongatus*, copepodite stage V of *C. finmarchicus*, *Oithona* spp., *Oncaea* spp., and small chaetognaths. The fish species inside the system are sprat, mackerel, cod, and pollock, as well as Cottidae, Labridae, and Gobiidae (Dahl *et al.*, 1973).

b) Lindås herring

Two herring populations have been identified inside Lindåspollene. One population represents the local Lindås herring (LPH) and the second is the NSSH. Decadal changes in body growth and number of vertebrae have been found between individuals of both populations. These adaptations were a result of the stock collapse in the late-1960s, when the NSSH changed its migration pattern, and became more confined to coastal areas (Johannessen *et al.*, 2014).

Generally, the total length of LPH adults ranges between 21 and 35 cm (25 – 30 cm, the most common); L_∞ increased from 31 cm in the 1950's to 32.9 cm in the 2000's (Johannessen *et al.*, 2014). LPH matures at age 2 and the maximum life span is around 20 years, although individuals older than 10 years are rarely found (Johannessen *et al.*, 2014). Fluctuations in L_{50} during three distinctive periods were described: from 1961 to 1964 females matured at 22 –

28 cm; from 1970 – 1982 there was a decrease in the length at maturation; 20 – 22 cm; currently, Lindås herring matures at around 26.5 – 28 cm (Johannessen *et al.*, 2014).

A small spatial segregation in LPH distribution was observed in Lindåspollene (Lie *et al.*, 1978). Prespawning LPH occurs in the deepest basin in the system (Spjeldnesosen; Langård *et al.*, 2014). LPH leaves the prespawning area at the beginning of March and moves towards the spawning grounds (Langård *et al.*, 2015). Spawning occurs in late March (around year day 90) in different areas in Lindåspollene. Feeding occurs close to the coast (Straumsosen and Spjeldnesosen) and overwintering in the northern parts of the Lindåspollene (Spjeldnesosen) (Dahl *et al.*, 1973; Østvedt *et al.*, 1973; Lie *et al.*, 1978). For a local population, LPH exhibits a high condition prior to spawning, high fecundity, and large oocytes (Silva *et al.*, 2013; **Paper III**). Fecundity ranged from 35 000 to 52 000 at 24 and 31 cm body length, respectively (Lie *et al.*, 1978), the current average fecundity for LPH is around 35 500 eggs at 1 320 μm (**Paper III**). Eggs are deposited on algae, pebbles, and rocks (Lie *et al.*, 1978; Johannessen, 1986).

1.2.2.7. Coastal Skagerrak herring

a) Strandfjorden system

Samples of CSH were collected in the inner part of Strandfjorden (southern Norway) (Fig. 10). Strandfjorden is a shallow (max. 13 m deep) and narrow fjord, which connects Skagerrak and Landvikvannet, via the Reddal Canal. During the spring, the water temperature inside the fjord ranges from 5 to 14°C and salinity between 10 – 25 psu (0 – 5m) (Eggers *et al.*, 2014).

b) Coastal Skagerrak herring

Adult CSH body size ranges between 22 and 34.5 cm, with an average of 28.3 (Eggers *et al.*, 2014), L_∞ reaches 31.3 cm (Eggers, 2013). CSH has a low number of vertebrae (56.6) and moderate growth rate (Eggers *et al.*, 2014). For a local population, CSH produces large eggs (mean = 1 325 μm) in large numbers (mean = 24 000 eggs) (**Paper III**). Spawning takes place in March-April.

1.2.2.8. Landvik herring

a) Landvikvannet system

Landvikvannet is an inland brackish lake, located in the southern part of Norway (Fig. 10). Water modification (freshwater to brackish) occurred after the opening of an artificial

channel, connecting the lake and Strandfjorden. Temperature inside the lake during spring ranges from 5 to 17°C (0 – 5 m), and the surface waters being less saline (1 – 7 psu) compared to the bottom (20 – 25 psu) (Eggers *et al.*, 2014). It is quite a shallow lake (average 4 m deep), but the entrance is 25 m deep (Eggers *et al.*, 2015).

b) Landvik herring

Scientific literature on this population is only available from 2013 (Eggers, 2013; Silva *et al.*, 2013; Eggers *et al.*, 2014; Eggers *et al.*, 2015). LVH is a semi-stationary herring population, that migrates into the lake to spawn (in March), with the main spawning occurring in May, and then leaves the lake shortly thereafter (June – August) (Eggers, 2013; Eggers *et al.*, 2014). The herring can inhabit the lake for over a month (Eggers *et al.*, 2015).

LVH is characterized by low numbers of vertebrae (56.1) and a slow growth rate (Eggers et al. 2014). The adult total length ranges from 23 to 34.5 cm (L_∞ of 30.3) and age from 2 to 12, but most of those caught were at ages 3 and 4 (Eggers *et al.*, 2014). This population shows high fecundity, on average 27 000 eggs at 1 220 µm are produced (Silva *et al*., 2013; **Paper III**).

Table 2. Overview of environmental parameters usually found in each fjord, and its respective herring population (Pop.) and biological parameters. D is the maximum depth, T is temperature, Sal is salinity, TL is total length (in cm), VS is vertebrae count, F_P is potential fecundity, and LC is leading cohort oocyte diameter. Additional information is described above.

Fjord	Location	D (m)	T (°C)	Sal (psu)	Pop.	TL (cm)	VS	F_P	LC
Lake Rossfjord	Northern	60	0 - 20	16 - 24	LRH	16.5 - 24.0	54.2	7500	1300
Balsfjord	Northern	195	1 - 8	32 - 34	BFH	24.0 - 30.0	55.0	14000	1200
Trondheimsfjorden	Western	500	3 - 15		TRH	24.0 - 29.0	56.4	23000	1200
Gloppenfjord	Western				GLH	24.0 - 32.0	56.1	26000	1150
Sognefjorden	Western	1300	7 - 8	34 - 35	SGH	19.5 - 28.5	56.3	19000	1100
Lindåspollene	South-western	90	5 - 7	30 - 32	LPH	21.0 - 35.0	56.7	35500	1320
Strandfjorden	Southern	13	5 - 14	10 - 25	CSH	22.0 - 34.5	56.6	24000	1325
Landvikvannet	Southern	25	5 - 17	1 - 25	LVH	23.0 - 34.5	56.1	27000	1220

1.2.3. Pacific herring: British Columbia herring

The British Columbia herring (BCH) represents the Pacific herring studied in **Paper III**. A short description of this population is therefore provided. The British Columbia coast is split into six main regions: North Coast (NC), Haida Gwaii (HG) (formerly known as Queen Charlotte Islands), West Coast Vancouver Island (WCVI), Central Coast (CC), Johnstone Strait (JS), and Strait of Georgia (SG) (Fig. 11).
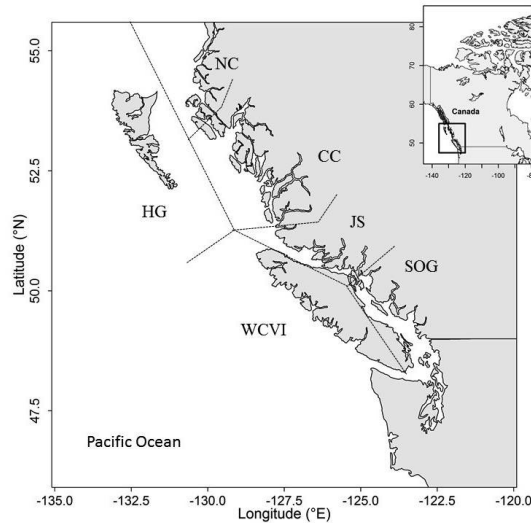
Figure 11. British Columbia regions: North Coast (NC), Haida Gwaii (HG), West Coast Vancouver Island (WCVI), Central Coast (CC), Johnstone Strait (JS), and Strait of Georgia (SG; map redrawn and modified from Hay *et al.* (2009)).

The British Columbia herring is distributed in inlets and fjords, and is believed to be composed of five main components: the southeastern coast of the Haida Gwaii, the north coast of British Columbia, the central coast of the Haida Gwaii, the north coast of Vancouver Island, and the Strait of Georgia (Hay *et al.*, 2001). Similar to all the Pacific herring, this herring spawns during the spring, from late February to early March or mid-April. Gonadal development starts in July-August, but oocyte development (vitellogenesis) intensifies after September (Hay, 1985).

The BCH is characterized by slow growth, small size (16 – 31 cm), small eggs, and high fecundity (Hay *et al*., 2008; **Paper III**). An average of 200 eggs per gram (whole body weight) is usually produced by this population (Hay *et al.,* 1985).

1.3. Life history strategies and tactics in and between herring populations

The most common life history traits are age- and length-at-maturity, adult size, life span, growth, condition, and egg production (egg number and size) (Stearns, 1992). Most of these traits have a direct or indirect role in fisheries assessment and management. Fish demonstrate a variability in life history strategies and tactics at all life stages (Stearns, 1992; Geffen, 2009). The variability is usually a response to endure adverse conditions, such as high mortality, climate fluctuations, scarce feeding conditions, and low population size (Rochet, 2000; **Paper I**).

The relation of two life history traits competing for the same resource to improve the fitness of one trait is known as a trade-off (Roff, 1982; Stearns, 1992). Stearns (1989) defined trade-offs on three levels: 1) genotypic level: genetic changes, 2) phenotypic level: traits related to reproduction and survival, and 3) intermediate structure level: this level connects both the phenotypic and genotypic levels. A total of 45 trade-offs were listed by Stearns (1989; 1992) with regard to growth, survival, reproduction, condition, and offspring production.

The allocation of resources to each metabolic activity is determined by the environmental conditions (Stearns, 1992). Fish, in general, demonstrate high adaptability in growth under environmental and ecological pressure. According to Roff (1982), "There are two extremes in patterns of allocation – First, a fish may maintain a constant body weight over time and adjust egg or sperm production accordingly. Second, a fish may produce a constant number of eggs and sacrifice body tissues to meet the requirements of production. Within these two limits a fish might, for example, sacrifice egg production at a rate that increases with decreasing body condition".

This thesis focuses mainly on the following trade-offs: 1) body size versus fecundity (**Papers I, II, and III**), 2) growth versus fecundity (**Papers I and III**), 3) fecundity versus egg size (**Papers I, II, and III**), 4) reproductive investment versus survival of offspring (**Paper II**). However, before getting into these trade-offs (see discussion for further information), a description of the herring life history strategies and tactics, focusing on the reproductive process, is given below.

1.3.1. Herring reproduction

Herring and most of the clupeids are generally characterized by late maturation, large body size at maturation, moderate reproductive investment, and low parental care compared to other fish species (Bone and Moore, 2008). Distinct reproductive tactics can be recorded at

the population level. The main differences are: a) spawning season and location, b) feeding season and strategies, c) reproductive tactics, and d) reproductive investment.

a)   Spawning season and location

Atlantic herring spawn all year, i.e. every population has a specific spawning season (Parrish and Saville 1965; Table 3; Fig. 4), whereas Pacific herring are exclusively spring spawners, i.e. spawning from late winter to early summer (see Blaxter, 1985).

Table 3. Examples of spawning season and spawning time in different Atlantic herring populations.

Spawning season	Herring population	Spawning time	Reference
Spring	NSSH	Mid-February – March	Kurita *et al.* (2003)
Summer	ISSH	July – August	Óskarsson and Taggart (2009)
Summer-Autumn	NASH	July –	**Paper II**
Autumn	NSAH	August – September	van Damme *et al.* (2009)
Autumn	West Scotland herring	Late August – October	Hay *et al.* (2001)
Autumn	Irish herring		Dickey-Collas *et al.* (2001)
Winter	NSWH	December	van Damme *et al.* (2009)
Winter	Celtic herring		Brophy *et al.* (2006)

A latitudinal gradient of the herring distribution with regard to spawning season has been identified: i) spring and summer spawners are located further north, ii) autumn spawners occur in the central areas, and iii) winter spawners are concentrated in the southern areas of the Atlantic Ocean (Iles, 1964; Melvin *et al.*, 2009). However, different spawner groups may overlap in their distributional area during the year, e.g. spring and autumn spawning herring in the Gulf of St. Lawrence (Messieh, 1975), spring and summer spawning herring in the Norwegian Sea and Norwegian coast (Husebø *et al.*, 2009; Pampoulie *et al.*, 2015; **Paper II**), autumn and winter spawning herring in the North Sea (van Damme *et al.*, 2009).

b)   Feeding season and strategies

The onset of maturation occurs when day length increases (McPherson and Kjesbu, 2012), and herring are found offshore accumulating energy resources (Hay, 1985 and reference therein). Overall, herring represent capital breeders, i.e. no food intake occurs during the spawning season (Slotte, 1999a). Likewise, appetite drops during the overwintering period. The energy stored during the feeding season is devoted to metabolic activities and gonadal development (Slotte, 1999a; Kennedy *et al.*, 2011). Varpe *et al.* (2005) suggested that

most of the energy accumulated during the NSSH feeding season is allocated to feeding migration, with 17% destined for body growth, overwintering, spawning migration, and spawning itself and only 7% of the energy accumulated is used to develop gonads.

Differences in food intake are found among herring populations during the different spawning seasons. The feeding season of ISSH, for instance, takes place in two periods: 1) during spring and summer before spawning, and 2) during the autumn, after spawning and prior to the overwintering period (Jakobsson *et al.*, 1969). The energy consumed and energy stored in each period is exclusively used for gonadal development and metabolic activities, respectively (Jakobsson *et al.*, 1969). Active food ingestion of NSSH starts at the spawning grounds (Slotte, 1999a; Axelsen *et al.*, 2000), and peaks between May and June, and again in August-September (Varpe *et al.*, 2005). Hence, apparently, no food is taken in the period after overwintering and before spawning in this study.

c)   Reproductive tactics

Oogenesis is divided into five stages: (1) production of oogonia (oogonial proliferation; OP), (2) primary oocyte growth, i.e. the transformation of oogonia into primary oocytes (folliculogenesis; primary oocytes are often labelled as previtellogenic oocytes; PVO), (3) formation of cortical alveoli oocytes (CAO), (4) vitellogenic oocytes (VO), i.e. vitellogenesis: accumulation of yolk protein, and (5) the final processes of maturation and ovulation: during this stage, oocytes rapidly increase in size due to hydration (Wallace and Selman, 1981; Lowerre-Barbieri *et al.*, 2011b). The recruitment of oocytes during oogenesis can be continuous (asynchronous) or discontinuous (group-synchronous and synchronous) (Wallace and Selman, 1981; Murua and Saborido-Rey, 2003; Pavlov *et al.*, 2009). In the latter case, fecundity is relatively easily determined, compared to the asynchronous type, where fecundity can be both determinate and indeterminate (Murua and Saborido-Rey, 2003). Thus, in all situations, the spawning can be total (a single batch spawned) or in several batches. These diverse fish reproductive concepts are properly described in the literature (e.g. Hunter and Macewicz, 1985; Hunter *et al*., 1992; Murua and Saborido-Rey, 2003; Pavlov *et al*., 2009; McBride *et al.*, 2015; Kjesbu, 2016). A summary of the main concepts used here is presented in Table 4.

Herring display similar reproductive strategies at the species level. Herring are a total spawners with determinate fecundity (Murua and Saborido-Rey, 2003; Kjesbu, 2016; see Table 4). Therefore, the number of eggs estimated prior to spawning reflects the final potential fecundity (Ganias, 2013). Herring also show a group-synchronous pattern, where

there is a gap between primary (PVO) and secondary (VO) oocytes. The secondary oocytes are recruited to be developed during the current reproductive cycle, whereas primary oocytes will be recruited at the next reproductive cycle (Hay, 1985; Murua and Saborido-Rey, 2003) or, potentially, even later (**Paper II**).

Differences in reproductive tactics among Atlantic herring populations have been recorded since the late 1930s (e.g. Farran, 1938; Baxter, 1959; Parrish and Saville, 1965; Hempel and Blaxter, 1967; van Damme *et al*., 2009; **Paper II**). As an overall pattern, summer and autumn spawners display small oocytes in large quantities, whereas spring and winter spawners produce large oocytes in relatively small numbers (Cushing, 1967; Hempel and Blaxter, 1967; **Paper II**). These differences in egg production are a consequence of the duration of gonadal development; winter and spring spawners stay longer in the vitellogenesis stage (Iles, 1964; van Damme *et al.*, 2009; **Paper II**), while summer spawners have a short gonadal development (Jakobsson *et al.*, 1969; **Paper II**). In quantitative terms (number and size of eggs), ISSH produces on average 136 000 eggs at age 6 (Jakobsson *et al.*, 1969) at 874 μm (average) prior to spawning (Óskarsson and Taggart, 2006). NSAH, on the other hand, produce ca 67 000 eggs at 965 μm, and NSWH, after down-regulation, ca 30 900 eggs at 1345 μm (van Damme *et al.*, 2009).

The down-regulation concept (DR; Óskarsson *et al.*, 2002) was initially introduced in NSSH (Kurita *et al*., 2003), but it seems to be a common strategy adopted by diverse Atlantic herring populations (e.g. Óskarsson and Taggart, 2006; van Damme *et al.*, 2009; Bucholtz *et al.*, 2013). During the maturation cycle, fecundity is down-regulated through atresia, which provides supplementary energy to conclude the oocyte development (Hunter and Macewicz, 1985; Hay and Brett, 1988). In NSSH, atresia activity takes place mainly in October and November, in oocytes with a diameter (OD) between 700 and 1 200 μm (Kurita *et al.*, 2003). For summer spawners, the high intensity of atresia occurs two months prior to spawning (May-June), in oocytes around 700 – 900 μm (Óskarsson and Taggart, 2006; Óskarsson and Taggart, 2009). The high intensity of atresia is mainly related to fish in poor condition (Óskarsson *et al.*, 2002; Bucholtz *et al.*, 2013). In a situation with an extremely low body condition, fish tend to skip spawning season (Rideout *et al.*, 2005; Rideout and Tomkiewicz, 2011), especially when individuals show Fulton's condition factor (K) < 0.7 (Óskarsson *et al.*, 2002).

Table 4. Terms and definitions related to fish reproductive biology.

Term	Definition	Reference
Synchronous	Presence of oocytes at the same stage of development (single oocyte group)	Wallace and Selman (1981); Murua and Saborido-Rey (2003)
Group-synchronous	Presence of two populations of oocytes: previtellogenic oocytes ("recruit") and vitellogenic oocytes ("clutch")	Wallace and Selman (1981); Murua and Saborido-Rey (2003)
Asynchronous	Presence of all oocytes stages, no predominant oocyte stage is observed	Wallace and Selman (1981); Murua and Saborido-Rey (2003)
Determinate fecundity	Potential fecundity is defined prior to spawning	Hunter et $al.$ (1992); Murua and Saborido-Rey (2003)
Indeterminate fecundity	Potential fecundity is not fixed prior to spawning, new oocytes are recruited, matured, and spawned during the spawning season	Hunter et $al.$ (1992); Murua and Saborido-Rey (2003)
Total spawner	Oocytes produced in the maturity cycle are spawned all at once	Hunter et $al.$ (1992); Murua and Saborido-Rey (2003)
Batch spawners	Oocytes are spawned in several batches	Hunter et $al.$ (1992); Murua and Saborido-Rey (2003)
Atresia	Disintegration and reabsortion of oocytes during development	Wallace and Selman (1981); Hunter and Macewicz (1985)
Down-regulation	Reduction in developing oocytes number during the maturation through the process of atresia	Óskarsson et $al.$ (2002)
Potential fecundity (F_P)	Number of advanced vitellogenic oocytes (eggs) produced per female, without subtraction of atretic losses	Hunter et $al.$ (1992)
Relative potential fecundity ($RF_{P,W}$)	Number of eggs produced per gram of body weight	Hunter et $al.$ (1992); Ma et $al.$ (1998)
Somatic relative potential fecundity ($RF_{P,S}$)	Number of eggs produced per gram of somatic body weight	Hunter et $al.$ (1992); Ma et $al.$ (1998)
Realized fecundity	Potential fecundity subtracting for atretic losses	Murua and Saborido-Rey (2003)
Stock reproductive potential (SRP)	Annual variation in a stock's ability to produce viable eggs and larvae that may eventually recruit to the adult population or fishery	Trippel (1999)
Total egg production (TEP)	Total number of eggs produced by the female spawning stock	Beverton and Holt (1957)

d)   Reproductive investment

The combination of fecundity and egg weight indicates the reproductive investment (RI) in fish (Kjesbu, 2016). RI responds to population density, food supply, and temperature (Stearns, 1992; Kjesbu *et al.*, 1998; Kjesbu and Witthames, 2007) (see discussion for further information).

1.4.   Total egg production and recruitment

Total egg production (TEP) refers to the total number of eggs produced by the female spawning stock biomass (Beverton and Holt, 1957), and is useful as a predictor of recruitment (REC) (Marshall *et al.*, 1998). REC has an important implication for marine fish management and assessment, and is directly related to the SSB (Pepin, 2016).

Several studies attempted to explain the causes of REC success or failure for a determinate fish stock. REC success has been determined by several environmental factors (Sætre *et al.*, 2002; Skagseth *et al.*, 2015). Sætre *et al.* (2002) identified three main parameters that promotes the recruitment success of NSSH: 1) warm temperature promotes faster growth in larval and juvenile stages; 2) low predation by Atlantic puffin (*Fratercula arctica*); and 3) strong winds promote faster drift to nursery areas. More recently, Skagseth *et al.* (2015) also correlated the existence of strong year classes of NSSH with the physical condition of the NCC: high temperature, low salinity anomalies (e.g. freshwater input), and strong south-westerly winds. The positive relationship with NCC may be one of the factors responsible for explaining high recruitment classes, even when the SSB is low. Conversely, the main causes of recruitment failure, in general, are: 1) poor egg quality (Karjalainen *et al.*, 2016), 2) suboptimal variation in environmental conditions (e.g. Toresen and Østvedt, 2000; Drinkwater *et al*., 2003; Arula *et al*., 2016), 3) lack of synchrony with zooplankton production (Hjort, 1914; Cushing, 1990), 4) predation and cannibalism (Bailey and Houde, 1989; Skaret *et al.*, 2015), and 5) competition (Corten, 1986).

2. OBJECTIVES

The overall goal of this thesis was to explore and synthesize existing and new information on reproductive strategies and tactics of the Atlantic herring stocks complex in the Northeast Atlantic. The objective was to clarify whether there are fundamental stock-specific traits. This topic is of interest in a life history theory context, but also for fisheries management, as some herring populations are highly vulnerable to fishing.

Paper 1: The aim of this study was to verify fluctuations in energy allocation and trade-offs in NSSH over the last 20 years. It focused on different trends in body growth, body condition, and reproductive investment relating these fluctuations to climate fluctuations, food availability, and density-dependent effects.

Paper 2: The main points addressed in this paper were to (1) compare reproductive tactics, including RI, of three herring populations showing different spawning season (spring *vs.* summer and autumn spawners); (2) compare interannual fluctuations in NSSH oogenesis and fecundity over the last two decades; and (3) show potential bias in the use of the generalized fecundity formulas to estimate TEP.

Paper 3: The aim of this study was to compare difference in body growth and reproductive investment between spawning seasons, and between local and oceanic herring populations, including local Norwegian, Atlantic (Northeast and Northwest), and Pacific (Northeast) herring.

3. SUMMARY OF PAPERS

Paper I:

This paper focuses on the effects of intrinsic and extrinsic parameters in the energy allocation and trade-offs in the life history traits of NSSH. The main life histories traits studied were growth (cohort-growth-in-length and -weight), condition (weight-at-length), and reproduction (investment in gonad weight (GW) and egg production). Trade-offs between growth and reproduction were observed. Over the last two decades, NSSH has invested more energy in weight and less in length, most likely in an attempt to save energy to be allocated to reproduction and other metabolic activities. A decline in cohort-growth-in-length was observed from 1999 to 2003, followed by an increase. Cohort-growth-in-weight, in general, increased from 1999 to 2008, then decreased. Fluctuations in herring and mackerel biomass, in conjunction with a fluctuation in zooplankton biomass were responsible for this trend. Weight-at-length showed similar long-term trends among length classes (29 – 36 cm), mainly decreasing in the first decade (1994 – 2004), and then increasing again (from 2004 to 2011). The weight-at-length in the last three years from the time series (2012 – 2014) showed a constant value. A continuous increase in gonad weight was observed from 1999 onwards, with a slight decrease for both gender in 2013 – 2014, during both overwintering and prespawning periods. Temperature, zooplankton availability, and density-dependent effects contributed to the changes in the weight-at-length and investment in gonads in over the periods and length classes. Neither interannual variation in the prespawning ovary weight nor statistical tests correlating the variation with environmental drivers were able to illustrate the real dynamic within the gonads. Detailed analyses showed clear trade-offs between fecundity and egg size. Even though, more energy was invested in GW, the $RF_{P,S}$ dropped by 31 – 42% (1999 and 2014) compared to years with high relative fecundity (1997, 2006 – 2008). Difference in egg size over the years was mainly investigated here. The onset of gonad development (appearance of CAO; OD $\geq$ 240 µm) was estimated and we demonstrated that the gonadal development in 2013-2014 started earlier (almost one month) than in the other years. Based on that, we applied the Q_{10} law and our results indicated that oocytes grew faster in females with low fecundity. In 2013-2014, the oocyte diameter was larger during the whole maturation cycle and after October in 1998 (maturity cycle 1998-1999). We also demonstrated that temperature was not responsible for the increase in the oocyte diameter in years with low fecundity.

Paper II:

Atlantic herring vary in fecundity both within and among herring populations. We demonstrated that spring spawners produced few large eggs, and autumn spawners produced many small eggs. Further, the reproductive cycle of NASH was described for the first time. This population has a short reproductive cycle with oocytes staying in the resting stage from July to March, followed by short vitellogenesis and hydration, that occurs from May to July. Special attention was given to the variation in NSSH fecundity over the last 20 years (1997, 1999, 2006 – 2008, and 2014). Two groups of fecundity were found: females producing many eggs (1997, 2006 – 2008) and females producing a reduced number of eggs (1999 and 2014). Therefore, females were classified as: 'poor- and good-seasons females' (P&GSF; low fecundity), and 'good-seasons females' (GSF; high fecundity). This difference in fecundity was associated with the lag effect (three years earlier) caused by the zooplankton biomass. Food availability is known to affect the current fecundity by the process of down-regulation, when oocytes are reabsorbed by atresia. However, it was also suggested that food availability affects the oogenesis by apoptosis (AP). This programmed cell death (= AP) is elevated in scarce food situations and reduces the number of small oocytes (standing stock of oocytes), hence affecting the number of future oocyte recruitment. After identifying these two groups of females, we showed the bias caused by using a general fecundity formula to estimate the total egg production, and suggested that a segmented fecundity formula (P&GSF formula and GSF formula) be used. A new tool was created to identify which segmented fecundity formulas should be applied to estimate fecundity and TEP. Anomalies in average Fulton's condition factor *vs*. TL (K_{slope}) proved to be a powerful tool in predicting NSSH fecundity based on food resource data. K_{slope} = -0.005 was determined as a threshold to select between the segmented P&GSF formula (≤ -0.005) and the segmented GSF formula (> -0.005).

Paper III:

This paper compares the differences in growth and reproductive investment of several herring populations distributed in both the Atlantic and Pacific Oceans. A total of eight local spring spawning populations distributed along the Norwegian coast, four oceanic Northeast Atlantic herring populations, one Northwest Atlantic herring population, and one Pacific herring (British Columbia herring) were investigated. Also, included was the Balsfjord herring (a local Norwegian population), which is known to be closely genetically related to the Pacific herring. Herring were compared at different levels: Atlantic vs. Pacific herring, between spawning seasons, within spawning seasons, oceanic *vs.* local populations, and among local populations. Differences in life history were demonstrated at all levels: 1) Atlantic *vs.* Pacific herring: Pacific herring have higher reproductive investment (higher OW and relative fecundity) than Atlantic herring, regardless of the geographic location (oceanic and local). 2) Within and among spawning season: summer and autumn spawners produce larger number of small eggs compared to spring spawners. Our results also showed that the local Norwegian herring populations have size-specific differences in potential fecundity, but like spring spawners, all these local populations also produced large oocytes (eggs). Both local Norwegian herring and the Pacific herring showed a higher somatic relative fecundity ($RF_{P,S}$) compared to the Norwegian spring-spawning herring, but lower $RF_{P,S}$ when compared to the summer-autumn spawners. 3) Oceanic NEA herring populations showed faster growth and larger body size compared to local Norwegian populations, except for the Lindås herring, Landvik herring, and Coastal Skagerrak herring. 4) The local Norwegian herring populations were grouped into three groups: a) Lake Rossfjord herring: small body size, low growth, and high investment in egg production, b) Balsfjord herring, Trondheimsfjord herring, Gloppenfjord herring, and Sognefjord herring: medium body size, average growth, and slightly higher relative fecundity and small oocyte diameter. The high fecundity and small egg size may be due to atresia that still occurs in this group, and c) Lindås herring, Landvik herring, and Coastal Skagerrak herring: large body size, fast growth, and low relative fecundity. Differences in the life history characteristics are due to differences in migration pattern, intermix with Norwegian spring-spawning herring, and the environmental conditions found inside each fjord. Broadly speaking, local Norwegian herring and eastern Pacific herring are characterized by smaller body size, shorter life spans, and higher relative fecundity (in this case, spring spawners) when compared to Atlantic oceanic populations, with a few exceptions.

4. DISCUSSION

The thesis demonstrated that Atlantic herring is a highly complex and plastic species. This also applies within a stock (NSSH). NSSH adjusted the energy allocation between life history traits to cope with fluctuating conditions, due to the increase of temperature and competition, decrease in food availability, and multiple increases and decreases in stock biomass. New tools were presented to minimize bias in TEP estimates by using food availability and anomalies in condition (K_{slope}) as proxies. All the results found in this thesis could potentially be used to improve management of the Atlantic herring.

4.1. Herring variability

From an overall perspective, we found different levels of differentiation among herring populations: interspecific, inter-population, between spawning seasons, and with regard to spatial distribution (**Paper III**). Atlantic herring differ reproductively from the Pacific herring, but have similar body morphology. The Pacific herring population (British Columbia herring) exhibited a slow growth, high body condition, short life span, and high fecundity per gram of somatic body weight (Hay *et al*., 2008; **Paper III**), while Atlantic herring are a more diverse group, differing in spawning season and spatial distribution (geographical location). Morphologically, oceanic populations are larger in body size with faster growth, and have longer life spans than most local populations. Exceptions are the Lindås herring, Coastal Skagerrak herring, and Landvik herring (see below). Four local Norwegian populations (Balsfjord, Trondheimsfjord, Gloppenfjord, and Sognefjord herring) showed similar body growth (length-at-age and weight-at-length). Lake Rossfjord herring represented the smallest sized and with the lowest growth population. Although, LRH showed high reproductive investment (**Paper III**). Differences in reproductive investment and tactics among herring populations are discussed below.

4.1.1. Spring *vs*. autumn spawners

Spring spawning herring (e.g. NSSH) produces relatively few, large eggs and autumn spawners (e.g. NSAH) produce many, small eggs (**Paper II and III**), this statement confirm previous studies (Hempel and Blaxter, 1967; Bradford and Stephenson, 1992). The divergence in egg size between spawning season may be related to the larvae survival ("match-mismatch theory"; Cushing, 1990). Temperature, food availability, and prey size influences the hatching period and larval growth for both spring and autumn spawners (Hufnagl and Peck, 2011). Spring spawners produce large eggs to provide sufficient energy

reserves in the form of egg yolk, because when the larvae hatch there is initially limited food supply (i.e. prior to the spring bloom) (Cushing 1967; Hempel and Blaxter, 1967). The spring bloom is short but intense (Sundby *et al*., 2016). There is therefore, an optimum period for spring-hatched larvae to start feeding and the benefit from the abundance of food that will favor their development (Cushing, 1990; Hufnagl and Peck, 2011). Big larvae show a preference for large-sized prey and grow faster when there is a high abundance of food, thereby improving their fitness and reducing their vulnerability to predation (Gamble *et al*., 1985; Paulsen *et al*., 2009; Hufnagl and Peck, 2011). The production of many smaller eggs by autumn spawners, on the other hand, is a strategy to match food availability and ontogeny (Gamble *et al*., 1985; Geffen, 2009). The high number of eggs is a strategy to "guarantee" larval survival despite the high natural mortality and predation during this period (Cushing, 1967; Hempel and Blaxter 1967; Hufnagl and Peck, 2011). The small larval size is compatible with the size of the prey; small larvae eat small prey (e.g. smaller copepods (cyclopoids) and microzooplankton), which limits their growth rate (Gamble *et al*., 1985; Figueiredo *et al*., 2005; Hauss and Peck, 2009). However, it has been demonstrated that after an initial growth spurt, North Sea herring larvae, stop growing in length, and instead invest in increasing their weight, in order to accumulate energy resources for periods of low food concentration (Hufnagl *et al.*, 2015).

Sinclair and Tremblay (1984) had a different hypothesis ("member/vagrant hypothesis"), and proposed that retention area and the timing of metamorphosis are the main reasons for the difference in egg size between spawning seasons. In "good" retention areas (area with abundant food), larvae grow faster and metamorphosis occurs prior to the overwintering, which is the case for spring spawners. However, in "poor" retention areas (areas with limited prey abundance), larvae grow slowly, and metamorphosis takes place after the winter period (from April). Therefore, producing at high number of eggs is a strategy against the high mortality and low growth rates during this period.

For both hypotheses (match-mismatch theory and member/vagrant hypothesis), food availability (size and quantity) is a main precursor for larvae size and survival rate. Hufnagl and Peck (2011) stated that larvae hatched from early-January to late-May and from early-August to late-October have higher probabilities of survival, although survival rates of spring spawners were suggested to be higher, due to more optimal environmental conditions.

Spring-hatched larvae survival decreases during the summer when predator abundance and activities are higher (Hufnagl and Peck, 2011). Mackerel was identified as an active predator of NSSH larvae (Skaret *et al.*, 2015), likewise cod and haddock for local (fjordic)

populations of herring (Johannessen, 1980). Cannibalism has been recorded for both NSSH (Prokopchuk, 2009) and NSAH populations (Segers *et al.*, 2007), which may have an effect on early life history survival and thus be a mechanism for variability in recruitment. Cannibalism was suggested as one of the main reasons for NSAH recruitment failure (i.e. lower larval survival than expected) during the early 2000s. The suggestion was that adults of winter spawning herring prey upon autumn-hatched larvae, when these adults are migrating towards the overwintering grounds and autumn-hatched larvae are drifting to the nursery areas in the southeastern North Sea (German Bight) (Corten, 2013). From the beginning of the 2000s there was a rapid increase in larval abundance in the southern Downs region (indicative of an increase in the contribution of this portion of the stock to the abundance as a whole) (ICES 2016a). This increase in abundance may provide some evidence to support Corten's (2013) hypothesis of an elevation in cannibalism during this time period.

4.1.2. Oceanic *vs.* local herring populations

As stated above, herring reproductive tactics change according to both the spawning seasons (**Paper II**) and within spawning season, e.g. among NSSH and the local Norwegian herring populations (**Paper III**). Distinct reproductive tactics have been found between herring populations, which aim to increase the larval survival (McQuinn, 1997). We demonstrated that all local Norwegian herring populations maintained the traditional reproductive tactics presented by spring spawners, i.e. large eggs. However, fecundity differed significantly among them (**Paper III**). Differences in fecundity, within the same spawning season, have often been related to the female body size (**Paper III**), but also due to latitudinal trend (Hay, 1985; Fleming and Gross, 1990), and/or migratory activity (Silva *et al.*, 2013). The last two parameters also have a size-dependent effect.

Size-dependent potential fecundity was recorded in the NEA herring populations (**Paper II**), as well as between the local populations along the Norwegian coast (**Paper III**). A positive relationship between fecundity and body size was also recorded in each population, although all the local Norwegian herring populations showed a narrow length distribution (**Paper III**). The population with small body size (e.g. Lake Rossfjord herring) showed a lower potential fecundity compared to populations with large body size (e.g. Lindås herring) (**Paper III**). The discrepancy in fecundity is related to the body cavity available in big fish, that allows them to produce more eggs (Koops *et al.*, 2004; Hixon *et al.*, 2014). In Pacific herring, a positive relationship was found, between egg weight and body length (Hay, 1985). This relationship also was observed in Atlantic herring (**Paper II**). A positive relationship

between egg weight and body length has been demonstrated also in other species, such as Atlantic salmon (Reid and Chaput, 2012).

It has been documented for Pacific herring that the number of eggs per body gram increases as latitude increases (Hay *et al.*, 2008). California herring produces the highest number of egg per gram of body weight (220 egg g^{-1}), followed by British Columbia herring (200 egg g^{-1}), then Alaska herring (150 egg g^{-1}) (Hay *et al.*, 2008). The same was observed, for example, between summer-autumn spawning Atlantic herring. NSAH produced 190 eggs per gram of somatic body weight, whereas NASH, produced 190 eggs per gram of somatic body weight (**Paper II and III**). This latitudinal gradient in fecundity has also been described in other fish species, such as Atlantic cod and sole, and Pacific salmon (Fleming and Gross, 1990; Thorsen *et al.*, 2010; Rijnsdorp *et al.*, 2015). American shad (*Alosa sapidissima*) displayed an inverse pattern. Fecundity decreases as latitude increases, because this fish allocates more energy in migratory activities to find better spawning grounds (Leggett and Carscadden, 1978).

Migration is a common behavior in herring, particularly in oceanic herring (cf. Norwegian spring-spawning herring). Migratory fish tend to be larger than non-migratory fish or fish with restricted migration patterns. In general, migratory species grow faster and mature later than non-migratory species (Roff, 1988). Atlantic herring populations were classified based on their growth and migratory behavior in: i) migratory populations with fast growth, ii) semi-stationary populations also with fast growth, and iii) stationary populations with slow growth (Silva *et al.*, 2013, see also **Paper III**). Energetic resources need to be partitioned between migration and reproduction (Dodson *et al.*, 1985; Varpe *et al.*, 2005), and a large proportion is allocated to migration (Varpe *et al.*, 2005). Therefore, migratory herring produce fewer number of eggs per gram of somatic tissue than stationary populations (Silva *et al.*, 2013; **Paper III**).

Adverse environmental conditions found in the different fjord systems (e.g. Hognestad, 1994; Eggers *et al.,* 2014) or long-term interactions with NSSH (Johannessen *et al.*, 2009; Johannessen *et al.*, 2014) can also explain this disparity in body size and fecundity among the local Norwegian herring populations. Each fjord exhibits adverse environmental conditions, e.g. a long period of ice cover (at least 6 months) (Hognestad, 1994), low zooplankton production, and fluctuating oxygen concentration (Dahl *et al.*, 1973). These parameters may limit the growth of herring and their egg production (e.g. **Paper I**). Local Norwegian herring are known for their low growth rates and lower length-at-age compared to oceanic Atlantic herring (Silva *et al.*, 2013; Mikkelsen *et al.*, 2016; **Paper III**). However, an interaction

between the resident local Norwegian population, known as Lindås herring, and the truly migratory NSSH resulted in a change in growth rate in LPH (Johannessen *et al.*, 2009; Johannessen *et al.*, 2014) after more than 20 years of intermixing. Currently, the metric characteristics are similar to those found in the NSSH (Johannessen *et al.*, 2014). An advantage for a fish population with a higher growth rate is, at least in principle, a higher survival rate and lower reproductive effort (Stearns, 1992). Populations with a large body size were showed to invest less in reproduction compared to small body size populations, like BFH and LRH (**Paper III**).

4.2. Norwegian summer-autumn spawning herring

The reproductive parameters of NASH were studied for the first time and because NASH represents one of the herring populations in this study (**Paper II and III**), a brief discussion of this population is presented, in order to fill knowledge gaps regarding the life history traits and reproduction cycle.

NASH exhibited similar morphometric features (total length, body weight, and body growth) to NSSH (**Paper II**). During the initial life stage of the Atlantic herring, spring spawned larvae tend to have a faster growth rate than autumn spawned larvae (Johannessen *et al.*, 2000). However, during the adult phase both NSSH and NASH showed a similar length-at-age and weight-at-length relationship, while NSAH showed a correspondingly smaller body size (**Paper II**). The similar body size and age of these two oceanic Norwegian herring populations is likely explained by the overlap in distribution over a prolonged period of time (Langård, 2013). McQuinn (1997) stated that sympatric spring and autumn spawning herring populations co-occur at the same feeding and overwintering areas. This was also the case for NSSH and NASH which had the same distribution area during the feeding seasons in the Norwegian Sea, and during the reported NSSH overwintering and spawning periods in Norwegian coastal waters (Husebø *et al.*, 2005; Pampoulie *et al.*, 2015; Slotte *et al.*, 2016; **Paper II**). NASH co-occurred with NSSH in both feeding (July) and NSSH spawning (February) seasons (Slotte *et al.*, 2016, **Paper II**). Therefore, based on the similar morphometric features and the overlap in distribution between these populations, NASH individuals caught in July were identified by using the distribution in leading cohort oocyte diameter and histology (**Paper II**; see below).

NASH shows a long resting period, with females in resting stage from July until March (Slotte *et al.*, 2016, **Paper II**). In May, NSSH and NASH gonads are at similar stages, thus making it difficult to distinguish between them (Aril Slotte *pers com*). Vitellogenesis and

hydration occur in a short time, from May to July. We reported that spawning starts in July, due to the presence of hydrated females and females with postovulatory follicles (POF) (**Paper II**). However, because vitellogenic females were also caught in July, we suggest that spawning is likely extend a bit longer (see **Paper II**). Similar gonadal development is known in ISSH, a summer spawner population. ISSH gonads rest for eight months, then the onset of maturation takes place at the end of March and spawning between mid-July and mid-August (Jakobsson *et al.*, 1969; Óskarsson and Taggart, 2009).

All NASH females were caught prior to spawning, and therefore, tracking of down-regulation was not possible. In the case of ISSH, atresia occurs mainly in May (Óskarsson and Taggart, 2006). Despite this, we demonstrated that NASH shows high body condition, high fecundity, and small egg size prior to spawning (**Paper II**), i.e. a tactic similar to those adopted by other summer-autumn spawning herring (**Paper III**).

4.3. Reproductive investment

New RI indexes, based on fish length and weight, were developed (**Paper II**) to compare reproductive tactics among the oceanic and local Atlantic herring populations (**Paper II and III**).

The reproductive investment overlaps between spawning seasons. However, in the case of spring spawners, oceanic herring populations showed higher RI compared to the local herring population (**Paper III**). Another interesting result was the difference in RI within summer-autumn spawners (**Paper II and III**). SFH and ISSH had higher average RI compared to both NASH and NSAH (**Paper III**). Bradford and Stephenson (1992) claimed that autumn spawners from the NWA herring populations have a higher reproductive investment compared to spring spawners, by producing high number of eggs. However, this is not completely true. In a comparison of the RI between of NSAH and NSSH, NSSH showed a higher average RI, likely due to egg weight (**Paper II**).

From a long-term perspective, we noticed that NSSH and NSAH demonstrated a decrease in reproductive investment when comparing the period prior to the collapse of the stocks and recent years (2013 and 2014). The decline in fecundity seems to be the main parameter responsible for the decrease in RI, because almost no change in egg weight was observed prior to the stock collapse and at present (**Paper II**). NSSH currently produces eggs only 1% heavier than prior to the stock collapse (in the late 1960s), but with 50% less fecundity (see **Paper II**). Egg dry weight (EDW) of NSAH followed the same trend. Today EDW has increased 6% compared to the historical EDW estimated for the Buchan spawning

ground before the stock collapse, but decreased (~ 10%) for the Banks and former Dogger spawning grounds, whereas the fecundity at all spawning grounds decreased over 50% (see **Paper II**). It is important, however, to highlight that this comparative historical perspective in reproductive investment may be a realistic situation or perhaps just an interannual variation (plasticity) in the reproductive investment (fecundity) caused by scarce food supply (**Paper II**).

4.4. Norwegian spring-spawning herring life history traits

4.4.1. Trends in life history

Modification of life history traits represents a compensatory adaptation to the intra- and interannual environmental conditions (McQuinn, 1997). A diversity of factors has been documented to affect fish life history; fishing pressure, climate fluctuations, food availability, and density-dependent effects (e.g. Möllmann *et al*., 2005; van Beveren *et al*., 2014; Heino *et al*., 2015; Rajasilta *et al*., 2015) being the most common. Brett *et al.* (1979) stated that both abiotic and biotic factors must be considered when evaluating variation in body growth. In general, growth is a key life history trait and variation in its pattern may affect other life history traits (Dmitriew, 2011).

NSSH has changed the following life history traits: body growth, body condition, and egg production over the last 20 years (**Papers I and II**). These changes were mainly caused by temperature, food availability, and density-dependent effects. The effects of each parameter differed among the life history traits (**Paper I**). In the last ten years (2003 – 2014), NSSH have faced higher temperatures, lower abundance of zooplankton, and higher interspecific competition compared to previous years (1994 – 2002) (ICES, 2014c; ICES, 2015b). At the same time the SSB has fluctuated; peaking in 2009 and declining thereafter (ICES, 2015b). Increasing temperatures were also shown to affect the life history of NSSH, however its (parameter) effect was weak (**Paper I**). Temperature drives life history traits in different stages of the fish life cycle (Peck *et al*., 2012). Temperature may also have indirectly influenced the life history of NSSH, by affecting zooplankton biomass and species composition (Beaugrand *et al.*, 2002; Alvarez-Fernandez *et al.*, 2012; Kristiansen *et al*., 2016). The increase of temperature has been also proved for providing suitable environmental conditions for mackerel in the Norwegian Sea (Nøttestad *et al.* 2016a).

The negative effects of density dependence on body growth (**Paper I**) can be related to the amount of food consumed on the individual and/or population level and by competition for space (Brett *et al*., 1979; Shin and Rochet, 1998). Since 1995, these three pelagic stocks

(NSSH, NEAM, and BW) have expanded their distribution area in the Norwegian Sea during the feeding season, which has resulted in the increase of total pelagic stock size and scarcity of food availability (Utne *et al*., 2012a; see also **Paper I and II**). The abundance and distribution of mackerel have continuously increased in the Norwegian Sea (Utne *et al*. 2012a; Nøttestad *et al*., 2015). NEAM is an opportunistic species and preys upon similar food items as NSSH (Bachiller *et al*., 2016). In addition, mackerel overlap horizontally and vertically with both NSSH and BW in late summer (Huse *et al*., 2012b; Utne and Huse, 2012; Utne *et al*. 2012a). Mackerel biomass negatively affected NSSH body cohort growth. However, NSSH weight-at-length (condition) and gonad weight during both overwintering and prior to spawning periods were positively affected by the increase of NEAM biomass (**Paper I**). The effect of mackerel in NSSH energy allocation took place mainly after 2005, when the SSB doubled (**Paper I**). At the same time, NEAM body growth (length- and weight-at-age) and condition (weight-at-age) have decreased and it has been also caused by the density-dependent effects, i.e. herring and mackerel biomasses (Olafsdottir *et al*., 2016). BW, particularly juveniles, share the same horizontal area as NSSH, mostly in early summer (Utne and Huse, 2012), and an inverse pattern in SSB between these two stocks was observed (ICES, 2015b). BW, however, showed some (parameter) effect on the life history traits of NSSH. Overall, this density-dependent effect indicated that the Norwegian Sea has probably reached its carrying capacity (Huse *et al*., 2012a).

These trade-offs caused by environmental and density-dependent effects are not exclusive to NSSH nor do they only occur in the Norwegian Sea. These effects have been shown to affect initial stages (egg/yolk sac and larvae) of Pacific herring (Reum *et al*., 2013), adults of different Baltic herring populations (Möllmann *et al*., 2005; Rajasilta *et al*., 2015), and other short-lived clupeids in the Mediterrean Sea (van Beveren *et al*., 2014; Brosset *et al*., 2017). The reduction of the Baltic herring body growth and condition has been associated with a decrease in *Pseudocalanus* sp. biomass, as well as an increase in interspecific density-dependent competition with sprat (*Sprattus sprattus*) (Möllmann *et al*., 2004; Möllmann *et al*., 2005; Casini *et al*., 2011). Similar reduction on body size and condition have been recorded to occur in sardine and anchovy in several parts of the Mediterranean Sea (Brosset *et al*., 2017). In the Gulf of Lions (Mediterranean Sea), for instance, changes in the small pelagic fish composition, due to the increase of sprat abundance, negatively affected both sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) body growth, body condition, size, and age (van Beveren *et al*., 2014). These changes in life history traits created a cascade effect in the dynamics of these species, resulting in a reduction of the length at first maturity, higher effort

in reproduction, and the absence of old fish in the stock (van Beveren *et al*., 2014; Brosset *et al*., 2016b). Two aspects have been related for having caused these changes: 1) high fishery pressure on the sardine and anchovy, and 2) the lack of interest in fishing sprat, hence the high competition for food. These three small pelagic fish species share the same niche. However, sprat is a more opportunistic species, which has caused more pressure on both the sardine and anchovy (Brosset *et al*., 2016a). Even though affecting these pelagic fish species, a negative effect in growth has been also recorded for sprat in the area (van Beveren *et al*., 2014), being, therefore, similar to the finding for mackerel in the Norwegian Sea (Olafsdottir *et al*., 2016).

4.4.2. Trade-offs among body growth, body condition, and egg production

Feeding conditions determine how the energy will be allocated in the life history traits, as well as for the trade-offs among traits (Roff, 1982; Stearns, 1992; Karjalainen *et al*., 2016). Trade-offs between growth and fecundity negatively affect fish survival (Ware, 1982; Reznick, 1985; McBride *et al*., 2015), but positively affect the future recruitment rate (Shin and Rochet, 1998). Atlantic herring have been shown to invest less in body size in order to maintain high body condition, and to invest more in reproduction when food is limited (Rajasilta *et al*., 2015; **Paper I**). For other small clupeids (sardine and anchovy), similar patterns were observed – decline in growth and higher effort in reproduction. However, for these clupeids body condition also decreased, which compromised adult survival after spawning. As a result, these populations are now composed of young and small sardines and anchovies in the Gulf of Lions (Brosset *et al*., 2016b). As a capital breeder (e.g. herring and sardine), all energy stored during the feeding period will be utilized for metabolic and reproductive costs (Slotte, 1999a; Kennedy *et al*., 2010). However, some energy must be saved for the migration to the feeding areas after spawning (Rijnsdorp, 1990). Body condition plays a positive role on the quality of both ovary maturation and fecundity in herring (Óskarsson *et al*., 2002; Kennedy *et al*., 2010; Bucholtz *et al*., 2013). Condition is also a key predictor of the dynamics of fish stocks (Casini *et al*., 2011) and is a good indicator of reproductive success (Wootton, 1990). **Paper II** showed that reproductive success is a consequence of both previous food intake and current fish condition, and even in good body condition, NSSH may produce lower number of eggs (see below).

4.4.3. Trade-offs between egg number and size

Clear interannual trade-offs between fecundity and egg size was recorded in NSSH (**Papers I and II**). NSSH showed changes in fecundity and egg size compared to the past 20

years of their reproductive estimate (Óskarsson *et al.*, 2002; Kurita *et al.*, 2003; Kennedy *et al.*, 2011; summarized in **Paper I and II**). NSSH has recently produced larger oocytes in lower numbers (in 2014, and also in 1999), instead of producing many small oocytes (e.g. from 2006 to 2008). The same interannual trade-off between fecundity and egg size was also seen in NSAH, but has not been investigated further. In 2013, for example, the NSAH produced on average 36 400 eggs at 1 265 µm (**Paper II**), whereas in 2006 – 2007 an average of 65 700 eggs at 965 µm (van Damme *et al.*, 2009).

Trade-offs between fecundity and egg size appears to be a normal feature in fish, mainly influenced by environmental and food ration conditions (Tanasichuk and Ware, 1987; Ma *et al.*, 1998). Two different scenarios in relation to this trade-off were associated with prey availability (Winemiller and Rose, 1993). First, in poor prey conditions, a small quantity of large eggs is produced. Second, in high prey conditions, small eggs are produced in large quantities. In both scenarios, the aim of the adopted strategy is to promote high larval survival (Winemiller and Rose, 1993).

NSSH produces large eggs when fecundity is already low (**Paper I**). During the years with low fecundity, the daily oocyte growth rate was higher compared to years with high fecundity, however this faster growth was not a consequence of increase in temperature (**Paper I**). This strategy may be related to the fact that non later up-regulation (i.e. continuous recruitment of new oocytes to mature) is possible in herring (determinate fecundity species, see Table 4). Thus, as the number of eggs is already low, the best option is to invest in larger eggs to improve the probability of eggs survival and larvae fitness (see Iguchi *et al.*, 2012). An experimental studied (Iguchi *et al.*, 2012) showed that in low food situations, females reduce their growth to produce larger eggs thereby increasing the ability of the offspring to find food.

Several advantages have been related to the production of large larvae ("Big is better theory"; Miller *et al.*, 1988). The essential point is to increase the chances of recruitment success (Folkvord *et al.*, 2009; Hufnagl and Peck, 2011; Karjalainen *et al.*, 2016). As an overall rule, large eggs produce large larvae with greater yolk storage at hatching compared to small eggs. This higher yolk supply may reduce starvation, and possible death, until the larvae begin to find food on their own ("critical period"; Hjort, 1914). Also, large larvae have better visual skills and can swim faster, thus increasing their chances of finding food and escaping predators (Miller *et al.*, 1988; Folkvord and Hunter, 1986; Hufnagl and Peck, 2011; Iguchi, 2012).

4.4.4. Oogenesis and final fecundity: a reflex of oocyte recruitment and food availability

As previously stated, feeding condition is known to affect the life history traits of herring, but it can also affect oocyte recruitment (**Paper II**). The effect of scarce food supply in the oogenesis and final fecundity was hypothesized (**Paper II**, see Fig. 12) at two different levels: 1) When the scarce food supply affects the oogonial proliferation and/or PVO recruitment by apoptosis (AP), and 2) When the scarce food supply affects the current maturation cycle, and vitellogenic oocytes (VO) are reabsorbed by atresia. Down-regulation (DR) by atresia is the most studied process (e.g. Hunter and Macewicz, 1985; Kennedy *et al.*, 2011; Silva *et al.*, 2013). However, both processes that down-regulate NSSH fecundity will be discussed.

First of all, the effect of poor food condition in the oogenesis is introduced. As an iteroparous species with group-synchronous ovary development (Table 4), two groups of oocytes are normally found in herring: i) a group of large oocytes (VO) that will develop and be spawned, and ii) a group of small oocytes (standing stock of oocytes, reserve fund group or PVO) that will be recruited in future maturation cycles (Wallace and Selman, 1981; Murua and Saborido-Rey, 2003; McBride *et al.*, 2015). PVO cells are always present inside the ovary (Pavlov *et al.*, 2009). Oogonial proliferation is usually intense during the regenerating stage, but can be found in all reproductive cycle (Widner *et al.*, 2013). The proliferation of new oocytes (oogonia) is controlled by apoptosis. Apoptosis acts also on PVO cells. The AP prevalence is usually higher in adverse environmental conditions (Thomé *et al.*, 2012).

Based on Thomé *et al.* (2012) aforementioned statement and our results (**Paper II**), we developed the following theory (see Fig.12): In a good feeding season, oogonial proliferation (OP) is high and AP rate is low. Hence, the number of PVO cells recruited in the next reproductive cycles will be higher. The inverse occurs in a poor feeding season, i.e. low OP and high AP, resulting in low PVO recruited. PVO are normally subdivided into three phases based on the presence of the circumnuclear ring (CNR), and these phases represent the previous stage before the presence of CAO (Kjesbu *et al.*, 2011; McPherson and Kjesbu, 2012). The phases were called small PVOs (S), medium PVOs (M), and large PVOs (L; **Paper II**). As oocyte development is a continuous process, large PVOs will become CAO during the same period (Gunnarsson *et al.*, 2006), concomitantly M PVOs will become L PVOs and, S PVOs will become M PVOs (**Paper II**, see Fig. 12). The current L PVOs (i.e. CAO) represent the oocytes recruited to mature (Ma *et al.*, 1998; Kurita *et al.*, 2003), and its recruitment takes place after the spring equinox (McPherson and Kjesbu, 2012), whereas the

other PVO phases continue their development to be recruited in subsequent cycles. We, therefore, suggested that if during the oogonial proliferation, herring was affected in a given year by poor food condition, the low PVO recruitment will be observed for the next three to four reproductive cycles (cascading effects for PSF; Fig. 12 (follow the red letters)), when all PVO phases will finally develop into CAO, and therefore recruited to mature (**Paper II**).

The second down-regulation in fecundity, due to the low food intake, takes place during the current reproductive cycle (Hunter and Macewicz, 1985; Witthames and Walker, 1995; Kennedy *et al.*, 2008). The initial number of oocytes (CAO) recruited to mature is determined during the feeding season; however, this number is down-regulated through atresia in the maturation process (October – November; Kurita *et al.*, 2003). This process is already well known in fish, such as the Atlantic herring (e.g. Óskarsson *et al.*, 2002; Kurita *et al.*, 2003; van Damme *et al.*, 2009; Kennedy *et al.*, 2011). Atresia's role is to regulate the fecundity to enable fish to produce higher quality eggs and provide energy supply to continue the oocyte development (Hunter and Macewicz, 1985; Hay and Brett, 1988). However, the intensity of atresia seems to be higher in years with low prey availability (**Paper II**), and higher in years with high fecundity and small eggs size (**Paper I**).

We demonstrated (**Paper II**) that these two processes: AP acting during new cells proliferation (OP) and atresia during the vitellogenesis stage, contributed to reduce the NSSH fecundity, mainly in years with low food conditions. Our theory was supported by the literature (e.g. Kurita *et al.*, 2003; Kjesbu *et al.*, 2011; McPherson and Kjesbu, 2012; Thomé *et al.*, 2012) and results obtained (**Paper II**). Hence, we suggest that further studies on OP are needed to confirm our theory.
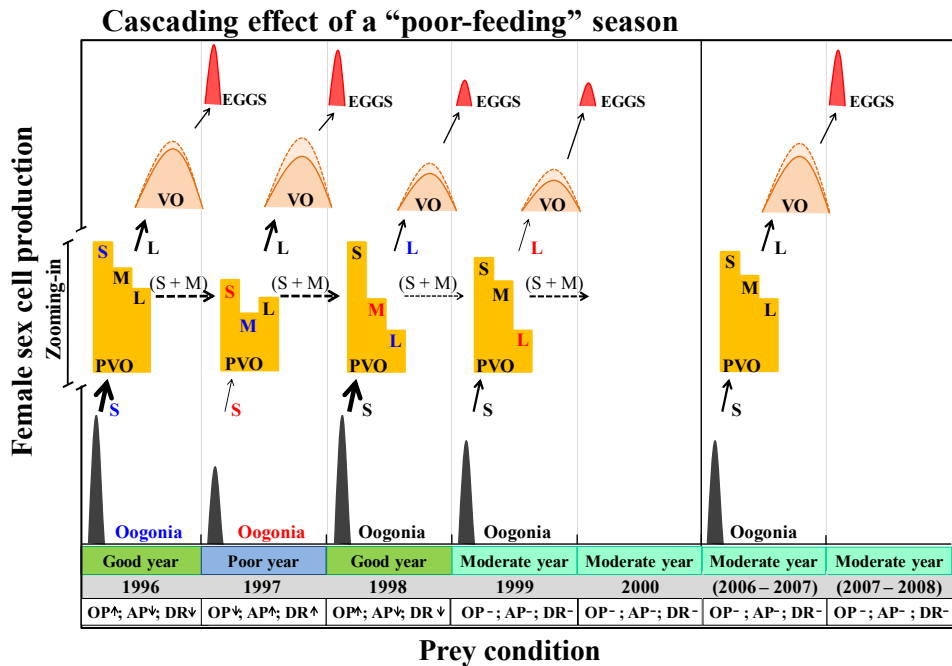
Figure 12. Schematic outline of how past and intermediate feeding seasons may affect females sex-cell production in NSSH, exemplified by tracking of a cohort of such cells following either a good (1996: blue letters) or poor season (1997: red letters). We suggest that the noted low fecundity (F_P) in 1999 (moderate season) was due to reductions in existing medium-sized PVOs in 1997 [M; circumnuclear ring (CNR); a structure rich in RNA and organelles] (McPherson and Kjesbu, 2012), whereas the potentially low F_P in 2000 (moderate season) was due to fewer, recruiting, small PVO (S; homogeneous cytoplasm) (McPherson and Kjesbu, 2012) in 1997. Therefore, in both cases 1997 had significant, negative influences on early oocyte recruitment reported as numerical production (EOR_N). M is known to switch rapidly into large PVOs (L; peripheral CNR, i.e. immediate before the CAO stage) at increasing day length in spring (Kjesbu *et al*., 2010; McPherson and Kjesbu, 2012), while down-regulation (DR) of vitellogenic oocytes (VO) is accelerated at low body reserves (which should be particularly high in late 1997) (Óskarsson *et al*., 2002). Note that width of the different types of frequency modes does not reflect reality, in particular the VO mode is much broader than the one for PVO (cf. "zooming-in" for this category). For oogonial proliferation (OP), apoptosis (AP), and DR arrows indicate direction of change (up or down), while hyphens a moderate impact. (Figure caption copied from **Paper II**).

4.4.5. Fecundity and TEP estimates

The morphometric parameters (TL, W, and K) are good predictors of fecundity (Bucholtz *et al*., 2013). Fecundity formulas were created using these morphometric parameters. However, we recorded that both W and K showed the same results (**Paper II**). An interesting point recorded in **Paper II** refers to the misleading effects of group different time series data, i.e. years with high fecundity ('good-season females'; GSF) jointly with years with low fecundity ('poor- and good-season females'; P&GSF) on the fecundity estimate studies. For the entire time series analyzed, a general fecundity (GF) formula showed a very low coefficient of determination ($R^2 = 0.39$). The application of the GF formula demonstrated that fecundity may be overestimated in years with low fecundity and vice versa. Therefore, we created segmented fecundity formulas based on these two fecundity groups (P&GSF and GSF). The coefficient of determination increased abruptly when considering only GSF ($R^2 = 0.83$), but also increased, with less intensity, when considering only P&GSF ($R^2 = 0.43$) (**Paper II**).

The accuracy in fecundity estimates is important because fecundity is a proxy used to estimated TEP (Marshall, 2016). TEP is determined by the proportion of females in the spawning stock, spawning stock biomass, and relative fecundity (Beverton and Holt, 1957), with sex ratio and fecundity as constant proxies (Marshall, 2016). Marshall (2016) listed several reasons why both sex ratio and fecundity should not be used as (constant) variables. Among the reasons are interannual variation in sex ratio, age and size composition, and interannual variability in relative fecundity. Therefore, to obtain reliable estimates of SSB in the fish stock assessment, it is important to minimize the uncertainty in TEP estimates. One of the questions addressed in **Paper II** was 'how to provide a useful mechanism to estimate egg production?' To answer this question, we developed a tool to identify which segmented fecundity formula should be applied to estimate TEP in the most accurate way. At the population level of NSSH, Fulton's condition factor (K) has been increasing in the past few years, whereas egg production has fluctuated or declined (see above; **Paper I and II**). However, K_{slope} declined with increasing TL, even when K was high. This negative pattern was recognized before the stock collapse, and also more recently (e.g. 1999 – 2000, and from 2009), whereas during the collapse both K and K_{slope} showed positive trends. Therefore, K_{slope} reflected better the fecundity situation compared to K. Based on that, K_{slope} was used as a threshold to determine which direction we should take to estimate fecundity. For $K_{slope} > -0.005$ the use of segmented GSF formula is suggested, while for $K_{slope} \leq -0.005$, one might use the segmented P&GSF formula (**Paper II**). The application of this tool was found to be

essential in estimating current TEP, but also to reconstruct long-times series of TEP. We also demonstrated that the use of a general fecundity formula affect the TEP estimates by age class, mainly in years where strong age-classes were produced (e.g. 2004) (**Paper II**). Therefore, our results support that fecundity should not be used as a constant parameter.

4.5. New techniques introduced and old techniques "rediscovered"

As previously mentioned, new methodology, techniques, and indices (e.g. RI and K_{slope}) were introduced (**Paper II**). However, conventional methodologies (e.g. histology and autodiametric methods) were shown to be very important, flexible, and accurate tools in studies of fish reproductive biology. Old techniques (e.g. EDW) were also demonstrated to be good options to be reused (**Paper II**). Discussion will be provided about the methodologies used (**Paper II and III**) that improved the accuracy of our results. Similarly, for simple techniques that increase the parameters measured.

Firstly, it is important to highlight the importance of applying the leading cohort oocyte diameter and histology techniques to distinguish females of NSSH and NASH (see Fig. S6 in the **Paper II**). Because of the difference in spawning season, applying these techniques was the best way to identify which herring population the females caught in July 2013 and 2014 belonged to (NSSH and NASH). Leading cohort represents a detailed expression of the maturity stage (Thorsen and Kjesbu, 2001), while histology is the most accurate technique to confirm gonadal development (Lowerre-Barbieri *et al.*, 2011a). In addition, the histological slides provided us with information about gonadal development, such as the presence of POFs, where we could identify that some NASH had spawned, and thereby confirm that NASH starts to spawn in mid-July (**Paper II**).

Another technique that gave efficient results, was the use of fixed eggs to estimated EDW (**Paper II**). The 10% buffered formalin (= 3.6% buffered formaldehyde) is the best reagent to preserve oocytes; but can affect the oocyte size, although at lower magnitude than ethanol (Ganias *et al.*, 2015). **Paper II** and Hempel and Blaxter (1967) compared fresh EDW and preserved EDW (EDW$_{fixed}$). In both studies a difference of less than 1% was recorded, indicating many advantages in applying this technique in fish reproductive biology studies: 1) the use of preserved eggs can facilitate sampling logistics and sample storage (e.g. samples can be collected any time and are easily stored), thereby reducing the need to keep samples fresh (maximum 48 hours after sampling); 2) can optimize the laboratory activities, because after measuring the oocytes, they can be counted manually and stored in small cups to be dried; and most importantly 3) the reuse of additional biological information that it has not

been used for many years, and is essential to provide information about reproductive investment (**Paper II and III**). This method does not seem to be appropriate for species, such as gadoids and plaice, due to the water content. The reduction rate in EDW varied between 15 and 30% by using preserved egg (Hislop and Bell, 1987). Still, according to the authors, for this species it is best to use frozen eggs, as they do not differ in weight compared to fresh eggs.

The use of the gravimetric method to estimate fecundity was also a good solution for frozen ovary samples (**Paper II**), and to estimate OD using the oocyte packing density (OPD) formula (**Paper III**). The use of the autodiametric method is, however, strongly recommended for two main reasons: it is less time consuming and more precise information can be acquired (OD and LC oocyte diameter) (Thorsen and Kjesbu, 2001).

5. CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Addressing questions regarding the life history traits of different species and populations of Pacific and Atlantic herring has provided some indication of the complexity of this group. Our study corroborates with previous studies. We demonstrated that spring and autumn spawners show a distinctive reproductive tactics, and within spawning season potential fecundity is determined by fish length. Differences in other life history traits were also found among populations in relation to their geographical location (oceanic or local) and over time within a population.

To the best of our knowledge, this is the first time that several (n = 14) herring populations have been studied simultaneously in terms of life history. In addition, eight local Norwegian herring populations were included in this study. The actual number of local populations is unknown (Holst *et al.*, 2004), and consequently nothing is known of their life history traits. Further studies on other local Norwegian herring populations are needed to provide better understanding of the investment in reproduction and growth patterns between and within the populations.

While there has been a general improvement in the quantity and quality of the biological and morphometric data (e.g. weight, age, sex ratio, and maturity) that are used to estimate a stock's potential egg production, this is not the case for fecundity data (Tomkiewicz *et al*., 2003). Although, there have been relatively few studies undertaken, the quality of the fecundity data is very high (e.g. Tomkiewicz *et al*., 2003). The methods used are well established (e.g. Ganias *et al*., 2015), and more accurate and faster methodologies have been developed (e.g. Thorsen and Kjesbu 2001; see also Ganias *et al*., 2015). In our study, we developed new techniques and adapted existing ones that will improve future fish reproductive biology studies for other herring populations. The central database of the Institute of Marine Research (IMR) was a source of plentiful and high quality NSSH biological data, with associated past and current reproductive data (Óskarsson *et al*., 2002; Kurita *et al*., 2003; Kennedy *et al*., 2011). This enabled us to explore and understand how NSSH has adapted its life history traits over the past 20 years.

NSSH has invested less energy in body size, and more in body condition and reproduction. These changes came about as adaptations to cope with abiotic and biotic conditions in the Norwegian Sea, including the indicative of possible carrying capacity of the system (Huse *et al*., 2012a) and climate fluctuations (Mork and Skagseth, 2010). Changes in life history traits were also observed in other herring populations, such as Baltic herring (e.g. Möllmann *et al*., 2005; Casini *et al*., 2006; Casini *et al*., 2009) and Pacific herring (Doug Hay

pers com). Therefore, continuous monitoring in the life history traits of herring populations is thus highly recommended, especially egg production due to absence of long-time series data information.

The increased investment in reproduction observed in NSSH could be misleading, if it is evaluated only in terms of gonad weight and the gonadosomatic index. For example, average ovary weight was similar in 2008 and 2014. However, this was not the case with fecundity and egg size. In 2008, females were highly fecund and produced many small eggs, whereas in 2014, fecundity was low and large egg sizes were produced.

Fecundity showed to be more plastic than egg weight and size. Intraspecific variation in NSSH fecundity was observed in both long-term (e.g. prior the stock collapse and recent years) and short-term (e.g. past two decades) periods. In the past 20 years, fluctuations in fecundity were the result of both current and past food conditions. Poor food conditions during oogenesis increases the apoptosis rate of small oocytes, thus affecting the number of oocytes recruited to mature. This negative effect will only become apparent three-four years hence. As previously mentioned, our theory was therefore, developed based on existing published studies and our own results. We strongly recommend that long-term experimental and field studies be performed to verify how food conditions affect oogenesis in a given year, and consequently the future fecundity (3-4 years ahead).

We discourage the application of the general fecundity formula to estimate TEP as our findings suggested that based on these differences in fecundity it gives unrealistic results. We propose a new tool (K_{slope}) to be use as a proxy to determine which segmented fecundity formulas (P&GSF or GSF) should be used, when there is a lack of fecundity data. The value of K_{slope} can be easily determine from the relationship between total length and Fulton's K, and easily applied to estimate TEP.

In conclusion, the results presented here reflect a small proportion of the changes that have occurred in the life history traits of the NSSH. It is therefore recommended that further investigations should be undertaken in both the NSSH and other herring stocks. Our suggestions aim to improve the quality of the herring life history traits and reproductive studies.

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