# Otolith structure as indicator of key life history events in Atlantic cod (*Gadus morhua*)

## Christian Irgens

Thesis for the Degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
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*"Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles"*

- Stephen C. Stearns (1992)

If I ought to explain the essence of this doctoral thesis in one line, it would be:

*Otoliths are like Facebook – anyone can reveal your whole life history.*

# Scientific environment

The work presented in this thesis was carried out in the Fisheries Ecology and Aquaculture research group at the Department of Biology, University of Bergen and in the Research Group Demersal Fish, at the Institute of Marine Research, from 2011 to 2018. This work was co-financed by the University of Bergen and the Institute of Marine Research.

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Olav, you have provided invaluable support in project management and financing that allowed for costly experimental studies at IMR to take place. I am also very grateful for your efforts in reviewing my written work which have given me a steep learning curve in scientific writing. Also, I will never forget that you won in our swimming competition that I was so confident to win. Perhaps I will ask for a re-challenge in ten or twenty years, so I might have a better chance.

I would also like to thank all current and previous colleagues in the two research groups that I have been privileged to be part of; the Fisheries Ecology and Aquaculture Research Group UoB and the Demersal Fish Research Group at IMR. I have always felt welcomed and included, and have benefitted from everyone's influence, both academically and socially. I will particularly thank Audrey Geffen, Jane Godiksen, Julie Skadal and Hildegunn Mjanger for their expertise and advice on otolith analyses and interpretations.

# Abstract

Otoliths are remarkable recorders of the individual life history, as they can reflect the growth trajectory and may encapsulate marks related to ontogenetic, physiological and environmental events. Visible and chemical information from otoliths may provide novel insights related to encountered environmental conditions that are difficult, if not impossible, to achieve by other means. However, a prerequisite to accurately elucidate the background of each individual from interpretations of otolith characteristics, is to understand how ultimate-proximate factors influence the otolith formation process as such. Although the biomineralization process of otoliths is indeed linked to physiology and in particular to metabolic expression, both environmental conditions and ontogeny may affect otolith formation. There are still unresolved issues concerning the precise relationship between intrinsic and extrinsic factors, which may have confounding effects when aiming at fundamentally understanding the process of otolith formation. Hence, this may introduce uncertainties to the interpretation of otoliths in terms of the expressed growth rate, opacity pattern, otolith shape and morphology. This also highlights the importance of validation studies on commercial fish species where otolith characteristics are used to determine age and key life history events that may be essential to stock assessment and management.

This thesis thus aimed to resolve how two main life history events, i.e. juvenile settlement and initiation of sexual maturation, can impact the otoliths of Atlantic cod (*Gadus morhua*), combining both field data and experimental studies. I have further evaluated how underlying endogenous and exogenous factors may fluctuate during life history events, and to what extent this may influence otolith growth and shape.

Based on extensive sampling of juvenile cod during trawl surveys in the Barents Sea, settlement was found to have a significant effect on the otolith external morphology. Increased formation of lobe structures was evident during the pelagic stage. However, this process was markedly abrupted during settlement in the autumn. Further investigations of the effects related to environmental conditions revealed that summer temperatures in the Barents Sea were linked to otolith lobe formation. No differences

were found in otolith shape between sympatric juvenile Barents Sea (BS) and Norwegian coastal (NC) cod, suggesting that otolith shape is mainly defined environmentally rather than by differences in population genetics.

Furthermore, the production and release of gametes has previously been suggested to induce a transition in the otolith zone structure and the formation of so-called spawning zones which are frequently observed in adult BS and NC cod. This otolith characteristic is therefore operationally used in assessments of spawning stock biomass, i.e. to numerically separate sexually immatures and matures, although no previous studies have rigorously validated these structures. Thus, to elucidate this mechanism, we demonstrate experimentally how energy investment related to sexual maturation and spawning may affect otolith growth and zone formation. The impacts on otolith structure were only significant in individuals with high reproductive investments, while otoliths from those with low investments (e.g. in first-time spawners) did not differ from immatures. This suggests that the individual energy level, as a premise for metabolic activity, plays an important role in the formation of spawning zones, and thus largely depends on experienced environmental conditions. Low investment in reproduction may thus not necessarily induce spawning zones, or stated differently, presence or absence of presumed spawning zones may not necessarily always reflect the real reproductive history of an individual.

Altogether, this doctoral thesis demonstrates that important life history events affect otolith formation in cod. More specifically, this work exemplifies how otolith shape ontogeny in juvenile cod from the Barents Sea markedly changes during the settlement event. Importantly, this thesis also demonstrate that environmental factors influence the shape formation during early life, indicating a plasticity in the ontogenetically driven shape formation. Finally, it was shown that the act of reproduction not necessarily induce spawning zones and thereby telling that this characteristic might occasionally be a misnomer. Thus, the in-depth analyses and findings given in this thesis should contribute valuably to on-going efforts to increase the quality of otolith readings as a central part in fish stock assessments and management routines.

# List of Publications

## Paper I

**Irgens, C.**, Kjesbu, O.S. and Folkvord, A. (2017) Ontogenetic development of otolith shape during settlement of juvenile Barents Sea cod (*Gadus morhua*). ICES Journal of Marine Science **74**: 2389-2397

## Paper II

**Irgens, C.**, Kjesbu, O.S., Johansen, T., and Folkvord, A. (in review). Spatiotemporal differences in otolith shape in juvenile cod coupled to temperature variations in the Barents Sea.

## Paper III

**Irgens, C.**, Folkvord, A., Otterå, H., and Kjesbu, O.S. (in manuscript). Otolith growth and zone formation during first maturity and spawning of Atlantic cod (*Gadus morhua*).

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# Contents

# 1  Introduction

## 1.1 Life history knowledge in fish management

Knowledge about life history traits is important in order to understand the action of natural selection, which is key to explain evolution (Stearns, 1992). Life history theory explains the broad features of a life cycle that is relevant for the reproductive success and fitness of a species. Key life history traits that define life history strategy and ultimately fitness of freshwater and marine fish have been suggested to be age and size at maturity, maximum age and size, growth rate, fecundity, egg size and parental investment (King and McFarlane, 2003). These are recognized as underlying determinants for population responses to climate and ocean changes from environmental forcing (King and McFarlane, 2003).

Information on life history events and strategies have been increasingly acknowledged as important components to integrate and improve stock assessment models and thereby management (Young et al., 2006). Although more holistic approaches in resource management and conservation have been on the steps in recent years (e.g. ecosystem-based management), this has yet to be implemented in a wide scale due to a combination of insufficient abundance information on biotic components, difficulties in identifying ecosystem drivers and tradition (Shephard et al., 2015; Skern-Mauritzen et al., 2015). However, assessment of newly exploited species, or when costly surveys are not an option, the use of conceptual frameworks for management based on life history traits and strategies has been suggested as they could indicate probable responses in population abundance and demography to both environment and fishing impacts (King and McFarlane, 2003). However, anthropogenic impacts and climate changes have also been suggested to have a direct impact on life history traits of fish populations (Mangel, 1994; Rochet et al., 2000; Fudge and Rose, 2008). For example, several studies have suggested that fisheries may induce evolutionary responses in age and size at maturation and migratory behaviour (Ernande et al., 2004; Jørgensen et al., 2008; Heino et al., 2015). The fact that fish stocks change, adapt, and evolve, in some cases maybe faster

than previously assumed, emphasizes the importance to monitor and consider life history traits in fish stock assessment and ecosystem management. It also highlights the need to gain deeper fundamental knowledge on stocks resilience and plasticity to natural and manmade influences, with special regards to life history strategies.

## 1.2 Otoliths as life history recorders

### 1.2.1 Otoliths: Unparalleled structures in fisheries research

Calcified structures like bones, scales and otoliths, found in a wide range of marine organisms (including all teleost fish), have the potential to grow and incorporate permanent deposits throughout life acting as life history recorders. Seasonal variations in environment and individual physiology may affect the mineralization processes (i.e. growth rate and composition), that could induce annual increments reflecting age. In particular scales and otoliths have been extensively used in research on fish age, growth, and population structure for more than a century (Hjort, 1914), in addition to being essential in modern fish stock assessment and management (e.g. Yaragina et al., 2009b). Annual increments are therefore particularly clear in fish inhabiting environments with large seasonal variations, such as in "high latitude waters". Compared to other calcified structures, otoliths are less subjected to mineral resorption, and have therefore a unique capability to preserve deposited growth structures and elemental composition (Thorrold and Hare, 2002). Otoliths are currently the most used structure for age estimation of fish (Campana and Thorrold, 2001). After Reibisch (1899) first identified annual structures in otoliths as age indicators (in plaice, *Pleuronectes platessa*), the extraction of a large variety of additional information has been demonstrated from a large number of species in these rather peculiar ear structures. This includes chemical composition (Dannevig, 1956), periodic microincrements (Pannella, 1971), structural discontinuities (Campana and Neilson, 1985), non-periodic growth zones (Karlou-Riga, 2000) and otolith shape (Campana and Casselman, 1993), which all to some extent reflect information on individual phenotype trajectory and ambient environmental history.

## *1.2.2 Biological function of otoliths in the inner ear*

Otoliths are calcium carbonate ($CaCO_3$) structures that are formed extracellularly in the inner ear of teleost fish. The inner ear is a paired complex labyrinth structure embedded in the cranium on either side of the head that are sensitive to sound vibrations, accelerations, and directional movements (Wright et al., 2002). The labyrinth system is composed of three orthogonally arranged semi-circular canals connected to end organs (otic sacs), namely saccule, utricle and lagena, being filled with endolymph fluid (Schulz-Mirbach et al., 2011). Each otic sac contains a sensory epithelium (macula) and a calcified body, an otolith, that function by stimulating mechanoreceptor hair cells in the macula. In most fish, three pairs of otoliths can be distinguished depending on placement; sagitta (in saccule), lapillus (utricle) and astericus (lagena) (Schulz-Mirbach et al., 2011). Of these, the sagitta otoliths are typically the largest and are most commonly used for otolith studies (Campana and Neilson, 1985).

## *1.2.3 Mineralization of otoliths*

The otolithic membrane that fixes the otolith over the macula has been suggested to contribute to the mineralization of otoliths (Dunkelberger et al., 1980). Otoliths are formed through accretion of $CaCO_3$ crystals in the aragonitic form and incorporation of organic matrix fibres (mainly proteins) from ionic and organic components in the endolymph, deposited in concentric layers (Dannevig, 1956; Morales-Nin, 2000; Wright et al., 2002; Allemand et al., 2007). This process involves rhythmic variations in the incorporation of organic components, which leads to periodic variations in the optical density (opacity) of the otolith, where mineral and matrix rich zones appear translucent and opaque, respectively.

Periodic otolith growth patterns may be detected both on a microstructural and macrostructural level, where primary increments may reflect daily deposits (Pannella, 1971), and macrostructural zone patterns may display annual increments (annuli) reflecting age in years (Reibisch, 1899). In addition, some species in intertidal habitats have also been found to deposit increment patterns that display weekly, fortnightly or month periodicities (Pannella, 1971). Although, primary increments have been shown

to be deposited at a daily rate in several studies in different species (e.g. Marshall and Parker, 1982), studies have also found that this is not always the case, as both sub-daily increments and lack of daily increments may occur (Geffen, 1982; Campana and Neilson, 1985; Dougherty, 2008). However, it seems likely that the periodicity in increment deposition is linked, if not synchronized, to the endogenous circadian rhythm and/or to daily environmental cycles. Generally, primary increments are best detectable in the early life stages (with the use of light microscopes), and becomes less clear with age (Pannella, 1971; Morales-Nin, 1988).

Annual increments, termed annuli, are wider opaque and translucent zones that are linked to the seasonality in fish growth due to seasonal variations in the environment (**Figure 1**). In many species, annuli are often deposited throughout the entire life, and are commonly used for age estimation (Campana, 2001; Fablet et al., 2011). However, structural discontinuities or irregularities (also referred to as checks) in the microstructure may interrupt the succession of the seasonal increments, which could be mistaken for a conventional annual increment (Gauldie, 1987). This could occur due to various possible circumstances, either related to environmental changes which may be "passively" recorded in otolith deposits (e.g. Matta et al., 2010), or on the other hand, "active" impacts on the otolith accretion from individual behaviour or physiological changes that relates to specific life history events.
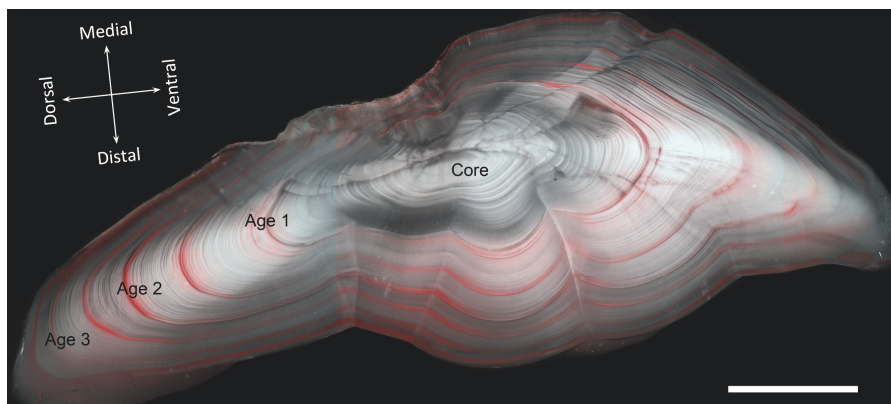
**Figure 1. Transversal section of an otolith of a 3.5-year-old Atlantic cod, reared in captivity and marked with alizarin (Paper III).** The otolith section displays the core and six alizarin marks embedded in six months intervals (from January and July each year) that verify ages from 1 to 3.5 years (birthday on 1 January). Scale bar 1 mm.

### 1.2.4 Otolith growth history

Otolith increments and growth trajectories have been used to estimate individual fish size at age and growth trajectory in many studies (e.g. Reay, 1972; Moksness and Wespestad, 1989; Sirois et al., 1998; Li et al., 2008; Wilson et al., 2009). Most back-calculation techniques are based on two underlying assumptions; a constancy of feature periodicity (i.e. daily or annual increments) and a proportionality between fish length and otolith size (Campana, 1990). However, both assumptions are susceptible to violations in many cases. Timing of seasonal increments have for example been shown to be related to geographical distribution, sex or year (Pearson, 1996; Høie et al., 2009), suggesting that periodicity (i.e. timing) could also change at the individual level (e.g. in long-migratory fish stocks). Furthermore, uncoupling between otolith and fish growth has also been demonstrated. In cases when optimal temperature for somatic growth was exceeded (Mosegaard et al., 1988), or when somatic growth almost fully ceased (Campana, 1983; Wright et al., 1990), otolith accretion was found to maintain at relatively higher rates than the somatic growth. A closer relationship has, however, been found between otolith accretion and metabolism, as the metabolic rate must remain

above a minimum maintenance level to sustain basal body functions during deteriorated growth conditions, and further, is positively affected by temperature (Mosegaard et al., 1988; Wright, 1991). Nevertheless, regardless of the inaccuracies that back-calculation techniques may introduce, the combination of otolith periodicity and growth trajectory provides a valuable tool in reconstructing estimates of individual body growth (or metabolic rate) that no other non-calcified structures (nor genetic or molecular approaches) can provide (Campana and Thorrold, 2001).

### 1.2.5 Impacts of life history events in the otolith growth structure

Sudden changes in the ambient environment, body ontogeny and physiology, which often characterize a life history event, will in many cases impact on the otolith formation (Geffen et al., 2002; Mosegaard et al., 2002). During early life stages, changes in the otolith microstructure, such as increment width and/or opacity, have been shown to provide precise information on timing of specific events or developmental stages, such as first feeding (Campana, 1983; Lagardere and Troadec, 1997), metamorphosis (Toole et al., 1993; Modin et al., 1996) and settlement (Wilson and McCormick, 1999; Vigliola et al., 2000). Additionally, the very first daily increment has been linked to hatching in several species (e.g. Clemmesen and Doan, 1996), while in others, they may be linked to other embryonic or larval developmental stages (Wright et al., 2002).

Particularly in long-lived species, life history events that typically occur later in life, such as sexual maturation or long-range migration, are often not possible to infer (or even detect) from microstructural analyses, as the number of (micro) increments decrease with age and become less visible (Pannella, 1971). However, it is much more common seeing marks from major life history events in the macrostructure pattern. Macrostructural settlement-marks, a type of discontinuity (or check) in a regulate seasonal zone, have for example been described in several species, including red gurnard (*Aspitrigla cuculus*) (Colloca et al., 2003), Baltic cod (*Gadus morhua*) (Rehberg-Haas et al., 2012) and various species of tropical reef fish (Wilson and McCormick, 1997). Settling marks have also been suggested as a possible source for misinterpretation of age because they may appear as false annuli (Gauldie, 1987;

Waldron and Kerstan, 2001; Rehberg-Haas et al., 2012). External factors such as reduced food availability and different prey type (Hüssy et al., 2003) or declined temperature (Toole et al., 1993) have all been suggested as probable causes to settling marks.

Studies by Rollefsen (1933) also pointed out that the onset of sexual maturation may induce a transition in the otoliths zone structure in Atlantic cod (*Gadus morhua*). By studying otoliths from both Barents Sea (BS) and Norwegian coastal (NC) cod, he identified transitions in the annual zone patterns that is described as a change from wide "inner zone" to markedly more narrow "outer zones", which assumedly reflects years with spawning. Similarly, transitions in otolith growth patterns have also been linked to sexual maturity in species such as plaice (Rijnsdorp and Storbeck, 1995) and orange roughy (*Hoplostethus atlanticus*) (Francis and Horn, 1997).

### 1.2.6 Metamorphosis and secondary growth centres

In addition to microstructural checks, secondary otolith growth centres (also termed accessory primordia) has been found to appear during the onset of metamorphosis (Campana, 1984; Toole et al., 1993). Once secondary growth centres emerge, growth increments are deposited around the growth centres and cause changes to the original growth directions from the primordium. This significantly affects the otolith shape formation in addition to complicate interpretations and analyses of growth increments (Wright et al., 2002). Since settling often occur shortly after metamorphosis, for example in flatfishes, the emerge of secondary growth centres is also argued to be linked to the environmental changes during settlement (e.g. Al-Hossaini et al., 1989). However, Modin et al. (1996) demonstrated experimentally that the onset of secondary growth centres (in plaice) is directly linked to the early stage of metamorphosis. In Baltic cod, secondary growth centres was also suggested to continue to emerge well into the juvenile stage, indicated by increasing number of lobe structures on the otolith surface (Hüssy, 2008).

## 1.3 The Atlantic cod

### 1.3.1 Ecology and life history

Atlantic cod is a commercially and ecologically important species with a wide distribution throughout the North Atlantic Ocean in predominantly demersal (or demersal-associated) habitats of nearshore waters or continental shelf areas (Brander, 1994; Frank et al., 2005; Hylen et al., 2008). Cod is a relatively long-lived strategist with considerable intraspecific stock dependent differences in terms of growth rate, timing and size at settlement, age-at-maturity, timing of spawning and life expectancy (Olsen et al., 2004b; Brander, 2005). The BS cod, for example, has a 'slow' life history as they become sexual mature at age 7-8 (ICES, 2017a) and may live up to 30 years (Rollefsen, 1953), although ages more than 20 years have been rare in more recent years (possibly due to higher fishing pressure). On the other hand, in the more southernly distributed cod stocks in the Celtic, Irish and North Sea region, faster life histories are evident, where maturation occur between age 2-3 and maximum age rarely exceeds 10 years (ICES, 2017b; ICES, 2017c). In addition to regional variation, temporal long-term changes in life history is also taking place. For example, a remarkable decline in age-at-maturity has taken place in several exploited cod stocks. This was argued to be caused by a fisheries-induced evolution (e.g. Jørgensen, 1990; Heino et al., 2015), but climatic changes has also been suggested as a driver (Nash et al., 2010).

Cod are highly fecund determinant batch spawners, with amount of eggs per season ranging between 200 000 and 31 million, depending on fish size and population (Brander, 2005). During the spawning season, which takes places between January and May (depending on population), eggs are released in up to 19 batches, fertilized and broadcasted into free water masses (Kjesbu, 1989; Brander, 2005). Like in other iteroparous species, trade-offs between growth and reproduction are constantly at play during the adult stage of cod (Lambert and Dutil, 2000; Folkvord et al., 2014). In cod, variations in growth and energy storage this is known to cause significant variations in both age-at-maturity and yearly reproduction. In fact, low energy also cause fish to skip spawning, i.e. not spawning in one or several subsequent spawning seasons once

spawning has commenced, an event that has been shown to frequently occur among cod populations, (Rideout et al., 2000; Hüssy et al., 2009; Skjæraasen et al., 2009; Rideout and Tomkiewicz, 2011; Skjæraasen et al., 2012).

There are basically three ontogenetic life stages in cod; embryonic, larval and juvenile/adult stage (Pedersen and Falk-Petersen, 1992). The early life stages and the transitions between them (i.e. hatching and metamorphosis), in addition time of first-feeding, all represent critical periods for survival and growth, and therefore crucial for future recruitment. Particular important for survival, is the timing of each stage or event, as this can determine food availability (e.g. the match/mismatch hypothesis, Cushing, 1990) and predation pressure (e.g. the 'bigger is better', 'stage duration' and 'growth-selective predation' mechanisms, see Hare and Cowen, 1997). Juvenile settlement is also a critical event in life, representing a shift from the pelagic "0-group stage", where the eggs/larvae and early juveniles more or less passively drift with the ocean currents, to a demersal associated stage, often in shallow or nearshore habitats, where the juveniles seek shelter, find different prey types, and become often more stationary. Exact timing of settlement, or at which body size, often play a role for post settlement survival (Juanes, 2007). However, in cod stocks, this information cannot be generalized, as timing of settlement is reported between May and October, and at size between 35 to 100 mm (Brander, 2005; Bastrikin et al., 2014).

Beside factors determining when juvenile fish will reach the nursery area, like time of spawning, and distance from spawning site (Bastrikin et al., 2014), the optimal timing of settling is thought to be influenced by density-dependent mechanisms, and trade-offs between mortality risk and maximized growth (Salvanes et al., 1994; Juanes, 2007). The use of otoliths to infer life history events, such as settling, maturation and spawning, may for example indicate timing of year, and at which age and size the fish encounter each event, which otherwise could be difficult to observe. This information may for example be essential in design of monitoring programs to avoid biases in abundance indices of 0-group fish and early recruitment (Dingsør, 2005), and to produce or update maturity ogives and monitor annual spawning stock biomass (Jørgensen, 1990).

### 1.3.2 Life history traits as "stock health" indicators

Variability in environmental conditions and climate forcing affect both life history characteristics and stock production (Øiestad, 1994; Stenevik and Sundby, 2007). However, fishing pressure may also induce significant changes to life history traits and stock structure, such as maturity-at-age and fecundity-at-age (Jørgensen, 1990; Olsen et al., 2004a), spawning migration and stock demography (Jørgensen et al., 2008; Opdal and Jørgensen, 2015). In worst case, rapid fishing-induced changes in life history may contribute to collapse of fish stocks, as in the case of the Northern cod off Newfoundland and Labrador in 1992 (Hutchings and Myers, 1994; Olsen et al., 2004a). Although the attribution of overfishing as the major cause to the collapse has been debated and thermal variations suggested as a contributing factor (Rose et al., 1994; Rose, 2004), there were clear signs of altered life history traits prior to the collapse; declined age-at-maturation, shortened spawning duration, increased fecundity and increased mortality (Fudge and Rose, 2008). As life history traits set the terms of individual fitness and thus ensure a productive fish stock, it is of fundamental importance to understand the impacts of both fishing and climate forcing.

### 1.3.3 The ecological and commercial importance of Barents Sea cod

A significant part of the work presented in this thesis has focused on the ecologically and commercially important BS cod. Historically, the BS cod (also referred to as Northeast Arctic cod, Arcto-Norwegian cod, and skrei) have had a major economic and cultural importance to many countries, in particular to Norway (Hylen et al., 2008). A widespread international trade of stockfish (dried cod), klippfisk (split, boned, dried, and salted cod), cod liver oil and cod roe has existed since the 17th century (Haaland and Svihus, 2011), but evidence also suggest that Vikings conducted large-scale production of stock fish in Lofoten, Norway, already in the 12th century (Sicking and Abreu-Ferreira, 2009). In modern time, the BS cod still have the status as one of the most commercially important fish stocks in the North Atlantic (Hylen et al., 2008), in addition to being a key species and an apex predator in the Barents Sea ecosystem (Bogstad et al., 2015). In contrast to the historically low levels of many other cod stocks,

the BS cod stock greatly increased in recent decades reaching historical high levels of spawning stock biomass due to ocean warming and strict management (Kjesbu et al., 2014), with a temporary peak in total stock biomass at 4 million tonnes in 2013 and consequently a total allowable catch quota of 1 million tonnes (Anonymous, 2012).

Since the pioneer studies on early life stages in cod in the late 19th century (Sars, 1867), the BS cod have become a highly studied stock in many research fields, including physiology, ecology, and genetics, in addition to studies on climatic and anthropologic impacts on population structure and general biology (e.g. Bergstad et al., 1987; Kjesbu et al., 1991; Stenevik and Sundby, 2007; Jørgensen et al., 2008; Star et al., 2011). Although, parts of the objectives in the early 1900s was to expand the cod and herring (*Clupea harengus*) fisheries beyond coastal waters (Sætersdal, 2008), this effort introduced a new era in the fishery science, with ground-breaking ideas on year-class strength and population dynamics by Johan Hjort (1914), which modern stock assessments and managements largely builds upon.

### 1.3.4 Life history characteristics of Barents Sea cod

The BS cod have several life history characteristics that differ from many other cod stocks. This includes settlement in relatively deep mid-oceanic conditions, long-range spawning migrations, high frequency of skipped spawning, and relatively slow growth rates (Bergstad et al., 1987; Otterlei et al., 1999; Skjæraasen et al., 2012; Opdal and Jørgensen, 2015). Generally, BS cod undertake spawning migrations of about 750 km, from the feeding area in the Barents Sea to the main spawning grounds along the coast of Northern Norway, where the majority spawn in the Lofoten area (Bergstad et al., 1987; Opdal and Jørgensen, 2015). In fact, BS cod have even been reported to migrate as far as 2000 km south of the Barents Sea, outside Vest-Agder in southern Norway, during a previous cooling period (Opdal and Jørgensen, 2015). Spawning takes place between March and May and the progeny of eggs and larvae are being transported north- and eastwards with the Norwegian coastal current and the Atlantic current (Pedersen, 1984; Sundby, 2000; Vikebø et al., 2005). As the larvae undergo metamorphosis entering the early juvenile stage during summer, they still remain

pelagic, in the upper 100 m as they are spread over large areas of the Barents Sea and west of Svalbard, 600-1200 km from their spawning grounds, before they settle in the autumn (Ottersen et al., 2014). This may represent a critical event in life as settled juveniles are often subjected to high predation pressure from larger predators, including older conspecifics (Dwyer et al., 1987; Yaragina et al., 2009a) and increased competition for food and space (Tupper and Boutilier, 1995b; Juanes, 2007). In addition, the introduction to a different habitat, with other prey types (e.g. Dalpadado and Bogstad, 2004) and physical conditions (e.g. Sundby, 2000; Hinrichsen et al., 2009) may also require physical and behavioural adaptations (e.g. Valen et al., 2016). The fact that cod juveniles all over the Barents Sea descend in mid-ocean conditions towards an ocean floor at 100–400 m depth that offers minimal light, low temperatures, little structural shelter and different prey and predator fields, illustrates how significant and critical this life history event may be.

### 1.3.5 Stock monitoring and otolith collection

Cod otoliths have been collected and archived annually since 1920 by the Institute of Marine Research (IMR), former "Norges Fiskeristyrelse" (Norwegian Fishery Investigations), although scarcely before 1933, as the most common medium for age reading was scales at that time. However, Rollefsen's (1933) investigations of cod otoliths marked the start of an extensive otolith collection program, as he found that age of older individuals were easier to interpret from otoliths compared to scales. Since then, the sampling effort gradually increased along with the developing fisheries industry and increased fishing pressure, and thus the need to closely monitor stock productivity. In recent years, more than 30 000 cod otoliths are collected and aged annually by staff at IMR, mainly from the BS cod, the North Sea cod, and the NC cod. To my knowledge, this collection of otoliths is the largest uninterrupted and most comprehensive archive of cod otoliths existing (**Figure 2**).

Considering the diversity of information types that can be extracted from otoliths through different methodological approaches, the otolith collection represents a unique possibility to study long-term trends in different aspects. Beside investigations on

population structure based on regular age interpretation (e.g. Ottersen et al., 2006; Zuykova et al., 2009), otolith archives opens the possibility to reconstructing ambient environmental history from otolith isotopes (e.g. Høie, 2003), discriminate between stocks from otolith growth and shape characteristics (e.g. Rollefsen, 1933; Campana and Casselman, 1993), and using micro- or macrostructural analyses to back-calculate individual size and growth rate (Otterlei et al., 2002; Hüssy et al., 2003) and indicate timing or age at life history events (e.g. Rollefsen, 1933; Rehberg-Haas et al., 2012).
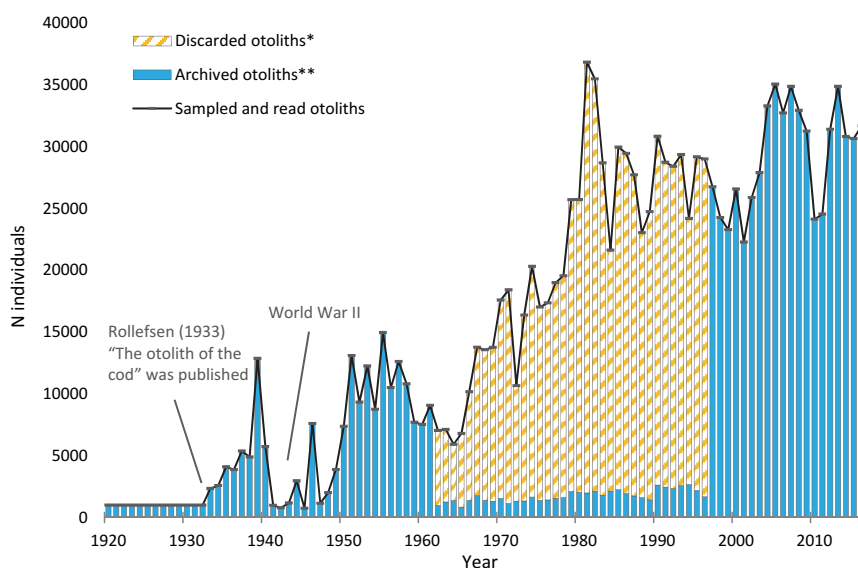


**Figure 2. Numbers of cod otoliths (otolith pairs from N individuals) collected and archived at the Institute of Marine Research, Norway.** The collection of cod otoliths first began in 1920 with approximately thousand samples each year. Pioneer studies on cod otoliths in the 1930s by Rollefsen (1933; 1934b; 1934a; 1935) and Dannevig (1933) showed that otoliths as a mean to determine age was more favourable than scales. After these discoveries, the sampling effort gradually increased in line with increased fishing efficiency and landings (Hylen et al., 2008). Disruptions in the otolith collections occurred during and after the World War II, and in the early 1960s. In the most recent decades, around 30 000 otoliths have been age read and archived each year. Unfortunately, in the period between 1962 and 1997, approximately 700 000 otolith samples (in total) were discarded after being read. *Numbers of

discarded otoliths between 1973-1979 are estimated based on the proportion of discarded otoliths in the other years. **The exact number of otoliths archived remains to be verified for years prior to 1932.

# 2 Motivation and study objectives

The potential to extract unique information on individual life history from otoliths is substantial with the broad repertoire of available methods and analyses that currently exists (Panfili et al., 2002), which also could be expected to expand in the future. This also highlights the value of longitudinal otolith collections such as the one at IMR (**Figure 2**) and justifies a continued effort in the years to come. However, to date, few sclerochronological studies have taken full advantage of this collection of cod otoliths from almost hundred years with sampling, as the main objective has been restricted to use age and age-at-maturity data generated from standard age-reading protocols in fisheries assessments (e.g. Jørgensen, 1990; Jørgensen, 1992; Yaragina et al., 2009b; Zuykova et al., 2009). This can be seen in connection with a lack of knowledge on how and to which degree, life history events impact the otoliths formation, in addition to a limited research focus on the in-depth understanding on the dynamics in life history traits and events. Also, the fact that the spawning zones defined by Rollefsen (1933) have not previously been validated, calls for precaution in their application as a sign of yearly reproduction.

Although, Rollefsen (1933) linked the transition in the otolith zone structure to the onset of sexual maturity, this assumption was based on several possibilities that do not necessarily reflect spawning *per se*, such as the migratory behaviour, reduced feeding and shift in habitat that is associated with the BS cod migrating to Lofoten. It was, however, also reported that spawning zones was only found in 60% of the presumably mature BS cod caught on the spawning grounds in Lofoten, which could indicate that spawning zones are not deposited (or visible) in all spawners. Furthermore, the possibility that settlement of BS cod could induce a settling check should also be examined, as this may provide information of timing and size at settlement. This could provide new insights into the settling process in the Barents Sea, which currently is not well understood, but potentially causes biases in 0-group indices (Dingsør, 2005).

To facilitate sclerochronological studies to elucidate life history events in the Atlantic cod, and to gain fundamental insights on topics such as life history theory and

evolutionary mechanisms in commercially exploited fish by utilizing available otolith collections, the overall objective of this doctorate work was to establish the relationship between life history events and phenotypic otolith characters in cod. In this thesis I focused on the two life history events in cod, namely settlement (**Paper I-II**) and sexual maturation (**Paper III**), that both have significance for stock monitoring, assessment and management, in addition to being critical stages in terms of recruitment and stock reproductive potential.

In order to assess the validity of the otolith characteristics that have previously, or currently, been linked to specific life history events, it was important to examine the relationship between intrinsic and extrinsic influences on otolith growth, opacity and shape formation. These goals were approached through both field investigations of temperature effects on otolith shape in juvenile cod (**Paper II**) and experimentally on the effect of spawning and feeding on the otolith zone structure (**Paper III**). In addition, the question about stock dependency in otolith growth and shape formation was addresses by examining otoliths from BS cod and NC cod. This was done experimentally where representatives from both stocks were reared in a common garden setting (**Paper III**) and through field studies of co-located juveniles from the two stocks (**Paper II**). More specifically this work aimed to:

- Examine otoliths from juvenile cod of the Barents Sea for settlement-related marks in the inner growth structure and impacts on the outer otolith morphology (**Paper I**)
- Investigate the relationship between regional and annual variations in environmental temperature and the otolith shape formation in sympatric BS and NC cod stocks (**Paper II**)
- Examine the relationship between otolith zone formation and reproduction (i.e. sexual maturation and spawning) and evaluate the validity of so-called spawning zones in otoliths from BS and NC cod (**Paper III**)
- Test for genetic effects on otolith shape, growth and zone structure between BS cod and NC cod (**Paper II-III**)

# 3  Abstracts of papers I-III

**Paper I:** This study documents how settlement of juvenile Atlantic cod (*Gadus morhua*) in the Barents Sea affects otolith growth and morphology. A simple method to objectively discriminate between age 0 and age 1 cod sampled in late summer was demonstrated by using only two otolith morphometric descriptors: area and perimeter. In the pre-settled 0-group cod, otolith lobe formation clearly increased with fish size, resulting in high otolith crenulation. This trend was disrupted during settlement, resulting in noticeably less crenulated otoliths of the settled 1-group cod sampled in winter. Combined observations of otolith shape, fish size, and body condition suggest that environmental factors associated with settlement during autumn, particularly reduced food intake, directly affect lobe formation leading to less crenulated otoliths. Comparably reduced body condition and otolith crenulation of 0-group cod in bottom trawls (vs. pelagic trawls) may indicate early settlement or vertical exploratory behaviour in the Barents Sea Ecosystem Survey (in August–September) and, thus, an underrepresentation of 0-group cod from pelagic trawling.

**Paper II:**  Environmental changes associated with settlement of juvenile Atlantic cod (*Gadus morhua*) has been suggested to influence otolith shape ontogeny. However, how environmental factors, particularly temperature and food availability, combined with the genetic contribution in different populations, influence otolith morphology is yet only briefly understood. Insight into the effects of short-term environmental fluctuations and long-term climate change on otolith development is essential for the operational use of otolith shape in stock identification, especially in mixed fisheries management. This study documented regional and annual variations in otolith lobe formation in juvenile Barents Sea cod from eight consecutive cohorts from 2005 to 2012. The lobe development during the pelagic stage of 0-group cod appeared positively related to regional temperature conditions but possibly also to food availability during this life phase. No difference was found in otolith shape between sympatric juvenile Barents Sea and Norwegian coastal cod, which indicates that

otolith shape is mainly defined environmentally rather than by potential differences in population genetics.

**Paper III:** Specific impacts of somatic growth, sexual maturation and spawning events on otolith zone formation in Atlantic cod (*Gadus morhua*) were assessed in a 33-mo tank experiment, using Barents Sea cod and Norwegian coastal cod raised under common garden conditions. High and low feeding ration combinations were used to mimic environmental stressors in the field. For both stocks apparent "spawning zones" in otoliths, defined as narrow annuli with a more pronounced translucent zone, are registered to estimate age at maturity, together with regular ageing and gonad maturity staging, thus adding relevant information to spawning stock biomass estimates. The present results showed that substantial energy investments in reproduction (approximated as fecundity per g body weight) caused reductions in the otolith growth and altered the proportional width between translucent and opaque zones within the reproductive cycle. These effects, however, were only significant among individuals with high reproductive investments, while the otolith structure in fish with low investments (e.g. in first-time spawners) did not differ from immature fish. Reproduction may thus not necessarily induce spawning zones, and spawning zones may not necessarily reflect reproduction. This suggests that the individual energy level, as a premise for metabolic activity, plays an important role in the formation of spawning zones, and thus largely depends on the environmental growth conditions.

# 4 Discussion

The potential for otoliths to record life history event rests on how intrinsic and extrinsic factors influence the otolith mineralization process, and how these factors may change before and/or during the events. The fact that life histories vary widely between cod stocks strongly suggest that "marks" in otoliths cannot be generalized to all cod stocks. This doctorate thesis has documented the relationships between otolith shape formation and settlement of 0-group cod in the Barents Sea (**Paper I-II**), and experimentally examined the relationship between reproduction and otolith growth and zone structure in BS and NC cod (**Paper III**). The findings in the first study (**Paper I)** resemble otolith shape characteristics that possibly are specific to juvenile cod in the Barents Sea. However, in the other two studies, the objective was to examine proximate factors that influence specifically otolith formation independently of stock origin, such as temperature effects on otolith shape during settlement (**Paper II**), and energy loss and feeding on zone structure during sexual maturation (**Paper III**).

## 4.1 Otolith growth and formation during settlement

### 4.1.1 Variability in settlement and otolith impacts

The transition from a pelagic to a demersal life stage have been shown to impact otolith formation processes in numerous species, and at different levels. Most attention has been brought to marks or transitions in microstructure or macrostructure growth patterns, as this can be used to estimate time of, and back-calculate fish size at, settlement (e.g. Wilson and McCormick, 1997; Wilson and McCormick, 1999; Vigliola et al., 2000; Wright et al., 2002; Rehberg-Haas et al., 2012). However, microstructural analyses have also shown that the otolith-fish size relationship may change during settling, challenging the reliability of back-calculation techniques during this stage of life (Campana and Neilson, 1985; Hüssy et al., 2003).

In the BS cod, however, macrostructural otolith analyses of settled 1-group individuals did not reveal settling-related marks or false rings, although settlement was hypothesised to impact the otolith growth due to the environmental conditions in the Barents Sea (**Paper I**). This contrasted previous studies on Baltic stock, where settlement was coupled to both microstructural checks and macrostructural secondary translucent zones (Hüssy et al., 2003; Rehberg-Haas et al., 2012). In fact, settlement marks in some Baltic cod could even be mistakenly interpreted as an annulus (thus also referred to as 'false rings') (Rehberg-Haas et al., 2012). On the other hand, settlement in the BS cod evidently coincided with a pronounced change in otolith morphology (i.e. reduction in crenulation from lobes) that was demonstrated with the use of basic morphometric parameters (**Paper I-II**). Paradoxically, this decrease seemed to contrast observations of undisrupted lobe formation in Baltic cod throughout the juvenile stage (Hüssy, 2008), suggesting stock specificity also in shape ontogeny. Apparent otolith phenotypic discrepancies between cod stocks may potentially be explained by both intrinsic and extrinsic factors. However, although cod stocks may genetically diverge (e.g. Fevolden and Pogson, 1997) stock differences in otolith growth and shape are often largely attributed to regional variations in environmental conditions (e.g. Otterlei et al., 1999; Bolles and Begg, 2000; Jónsdóttir et al., 2006a; Stransky et al., 2008a).

The amount of environmental stress experienced in a fish during a shift to a demersal habitat depends on many factors, including hydrographic conditions (e.g. gradients of temperature and light absorption), prey and predator fields, increased competition, substrate type, proximity to shore or shallow banks, and bottom depth. Considering the pan-Atlantic distribution of cod stock across a wide latitudinal range with contrasting environmental conditions, timing of settlement and size at settlement (Brander, 1994; Brander, 1995; Sundby, 2000; Brander, 2005), it is likely that potential settlement impacts on otoliths may vary between regions and stocks. This is further emphasized by the fact that stock differences are recognized by various features of cod otoliths, such as macrostructural growth patterns (e.g. Rollefsen, 1933; Rollefsen, 1934a), timing of annuli formation (e.g. Høie et al., 2009), otolith growth rate (e.g. Otterlei et al., 1999), otolith shape (e.g. Stransky et al., 2008a) and elemental composition (Jónsdóttir et al.,

2006b). Specific otolith features that may be linked to specific life history events in one cod stock should therefore not be generalized to all stocks without further investigations.

### 4.1.2 Otolith shape ontogeny during settlement

Changes in otolith shape have been linked to settlement in several species, however, these were primarily tropical coral reef fishes, where the changes have been attributed both as ontogenetic adaptations to the reef habitats and/or as a direct response to the post-settlement environmental conditions (e.g. Villegas-Hernández et al., 2008; Baumann and Gagliano, 2011; Vignon, 2012). However, settlement on tropical coral reef contrasts largely the biotic and abiotic properties of the demersal habitat types that cod may settle to, which including seagrass beds, rocky reefs, and muddy, sandy or cobble flats (e.g. Tupper and Boutilier, 1995a). The settling scenario in the Barents Sea shelf (of average depth of 230 meter) probably represents one of the most extreme contrasting habitat transitions seen among cod stocks in terms of depth and light conditions, and which obviously differs from settling conditions in tropical reefs.

Interestingly, otolith shape of BS cod was also found to markedly change during settlement (**Paper I**). Prior to settlement, the ontogeny of otolith shape was characterized by increased formation of otolith lobes in all growth axes of the medial plane (**Figure 3** and **4**). This trend corresponded with previous descriptions of otolith shape ontogeny in cod from a laboratory study, where lobe formation was connected to a progressing number of so-called secondary growth centres (Hüssy, 2008). The growth centres are known to first emerge during metamorphosis (Jearld et al., 1993; Modin et al., 1996), which basically transform the otolith shape from originally being circular at the larval stage, into a more elongate shape typical in adults (Hüssy, 2008). The close relationship between fish size, and number and size of lobes (**Paper I**; Hüssy, 2008), indicated an ontogenetic driven process of the shape formation. However, the growth and development of lobes were also influenced by environmental factors (**Paper II**; Hüssy, 2008; see discussion below).
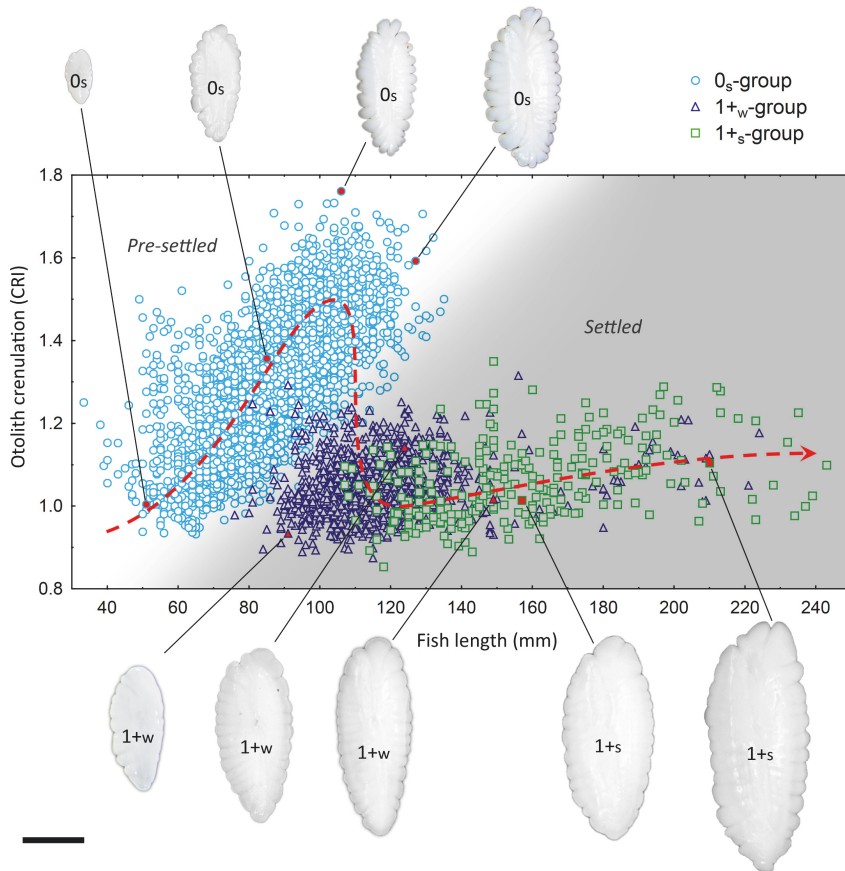
**Figure 3**. **Ontogeny of otolith lobe formation in juvenile Barents Sea cod.** The relationship between fish total length and otolith crenulation (CRI, indirect measure of lobe size and numbers relative to otolith size, see method description in **Paper I**) of the age groups; $0_s$-group ('s' for summer), $1+_w$-group ('w' for winter) and $1+_s$-group, is exemplified with respective otolith images. The dashed trend line indicates the direction of change in CRI with growth. Figure and text are modified from **Paper I** with additional data included from **Paper II**. All otoliths (images) are at the same magnification. Scale bar of 2 mm shown in lower left corner.

The positive relationship between crenulation and fish length in pelagic cod juveniles was however abrupted by a markedly decline in crenulation when comparing pelagic 0-group cod (from the BESS survey in August/September) with the newly settled 1-group cod (from the WS in February/March) (**Paper I**; **Figure 3**). Despite the large number of analysed otoliths, crenulation-fish length plot showed practically non-overlapping groups between the pre-settled 0-group cod and the post-settled 1-group when comparing within each cohort **(Paper I-II)**. Considering that shape formation is a gradual process that in its nature carried the previous growth/shape history along when being reshaped, observed abruption in lobe formations was regarded to be a remarkable change in shape given the relatively short period in time of five-months between the sampling periods of pelagic 0-group cod and settled 1-group cod. Interestingly, in contrast to the findings of abrupt lobe formation in the BS cod (**Paper I**), observations on juvenile Baltic cod suggests that lobe formation progress throughout the juvenile stage in Baltic cod (Hüssy, 2008).
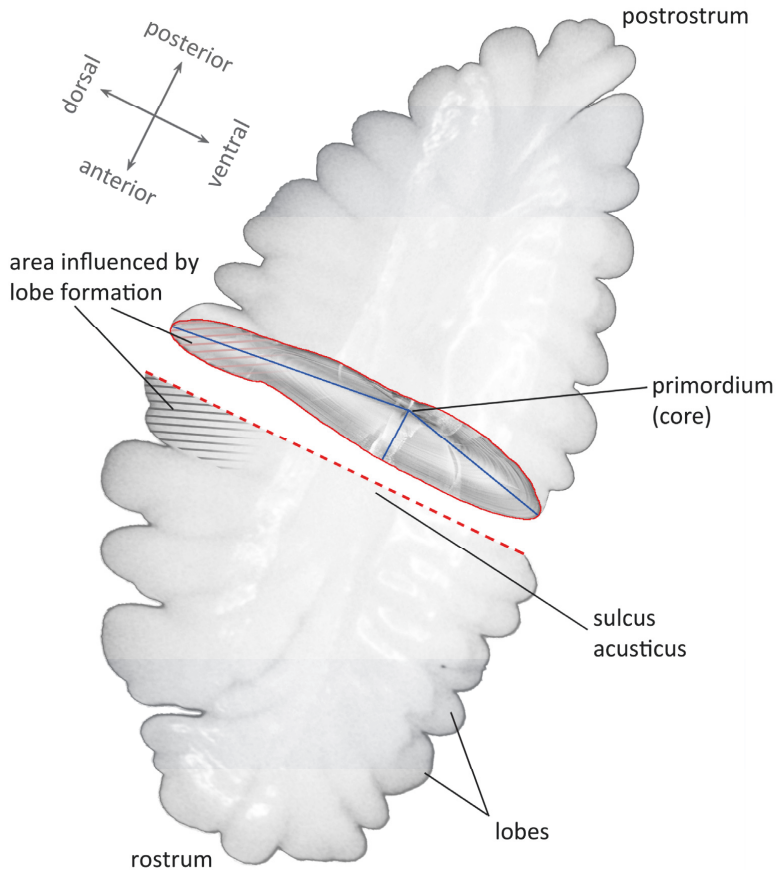
**Figure 4. Photographic illustration of a sagittal otolith of an 0-group cod prior to settlement (medial side facing up).** A hypothesised transversal cut (dashed line) is illustrated by a section enclosed by the curved solid line. Straight lines reflect radial axes for growth measurements. Lobe formation during the early juvenile stage prior to settlement is most distinct along the dorsal edge (shaded area). It should further be highlighted that the variability in lobe formation through juvenile stage (see **Figure 3**) may potentially cause biases to back-calculations of growth. The temporal variations in lobal growth vs. between-lobe growth, may cause inconsistencies in the growth trajectories depending on cut position, e.g. through a lobe (in illustration) vs. cutting in between two lobes.

### 4.1.3 The relationship between otolith morphology, function and habitat

The observed changes in otolith morphology of juvenile cod (**Paper I-II**) could be explained by a strong selection pressure on shape-based functionality in hearing and spatial orientation in relation to the settlement event. As light intensity rapidly dissipates with depth (Lythgoe, 1988), and prey and predator fields change (e.g. Ponomarenko, 1965; Dalpadado and Bogstad, 2004), a shift to a demersal habitat may require adaptations, both behaviourally (e.g. foraging, Lomond et al., 1998) and physically (e.g. sensory systems, Lecchini et al., 2005). Visual capability of cod have for example been demonstrated to change due to retinal development during metamorphosis, suggesting adaptations to the approaching shift in habitat (Valen et al., 2016). The auditory and vestibular roles of the otolithic organs of the inner ear (in sensing sound, balance and orientation), is therefore likely to require modification to a demersal life stage. Studies on auditory response in settlement-stage coral reef fish larvae have shown that hearing (besides olfactory sensing) aids in detection of proper settlement habitats (Wright et al., 2008). In addition, demersal species were shown to have more sensitive hearing than those in pelagic habitats (Wright et al., 2010). There is a clear trend that species inhabiting deeper habitats, thus specializing in auditory communication, have larger otoliths than those inhabiting epipelagic habitats where visual communication in more important (Cruz and Lombarte, 2004; Lombarte and Cruz, 2007). The relation between otolith morphology and functionality of mechanoreception and sound transduction has also been addressed and supported in numerous other studies (e.g. Gauldie and Nelson, 1990; Popper and Lu, 2000; Schulz-Mirbach et al., 2011; Inoue et al., 2013).

Cod use auditory communication during spawning using drumming muscles to set the gas-filled swimbladder into motion (Nordeide and Kjellsby, 1999), they exhibits a highly versatile migratory behaviour which includes pelagic migrations between (and within) nursery, feeding and spawning grounds (Neuenfeldt et al., 2013), and have relatively large otoliths. Altogether, this emphasize the importance otoliths have in orientation and hearing in the post-settled and the adult stage. Different from most other cod stocks, the BS cod settle to relatively deep demersal habitats with almost no available light (e.g. catches of settled 1-group cod from depths of >400 m are common,

materials in **Paper I-II**). In addition, the long northern winter that approach short after settlement offers limited daylength (in terms of light). Consequently, the visual conditions will also be highly reduced also in the shallower areas of the Barents Sea. This emphasize that settled cod in the Barents Sea must adapt to a deep and/or dark demersal habitat where hearing is essential for both prey detection and predator avoidance, and ultimately survival.

The observed reduction in lobe formation (**Paper I**) could therefore be an evolved adaptation of functional design to enhance sound reception, suggesting an ontogenetically driven lobe trajectory (**Figure 3**). On the other hand, Gauldie and Crampton (2002) suggested that increased complexity in otolith shape aids in hearing, as they found an increase in complexity of otolith shape in fish inhabiting deep-water environments compared to those in shallower habitats. This idea contradicted that fact that the complexity of the BS cod otoliths decreased during settlement, as the lobes became less pronounced and crenulation declined. In principle, there can be (at least) two explanations to why these findings contradict: i) the complexity of shape (being an imprecise definition) does not necessarily need to increase to enhance hearing, as for example relative otolith size also could matter; ii) the evident reduction in crenulation of otoliths in BS cod is not (or to a limited extent) ontogenetically driven by a pre-programmed shape-functional adaptation, but instead, expressed as a result of the environmental influences that the juveniles are subjected to during settlement (e.g. Sundby 2000; Hussy, 2008; **Paper II**), and thereby represents a cost that the juveniles simply must bear as a trade-off while seeking a demersal habitat.

### 4.1.4 Stock variability in shape: Environmental and genetic influences

Variation in otolith shape has been shown to serve as a marker of stock origin in numerous species (e.g. Stransky et al., 2008b; Yu et al., 2014; Brophy et al., 2016), including cod (e.g. Petursdottir et al., 2006; Stransky et al., 2008a). Although both genetic and exogenous factors influence the development of otolith shape, the relative contributions throughout life are not fully established (Bolles and Begg, 2000; Cardinale et al., 2004; Jónsdóttir et al., 2006a; Vignon, 2012; Berg et al., 2018). Both

feeding level (Hüssy, 2008) and sea temperature (**Paper II**) positively influence otolith lobe formation in juvenile cod. Considered that decreased body condition post settlement indicate a reduction in food intake (**Paper I**), in addition to a striking co-variability between the otolith lobe trajectory and the trajectory of ambient temperature of BS cod juveniles (**Figure 3** vs. **Figure 5**; Sundby, 2000), where both temperature and otolith lobal crenulation peaks prior to settlement, it is indeed clear that endogenous factors largely influence otolith shape. By any means, the observed lobe ontogeny strongly suggests that a markedly reduction in lobe expression may act as an indicator of settlement.

In contrast to the decline in otolith lobes in BS cod (**Paper I**), findings in an experimental study on cod juveniles of comparable size and age (stock origin is not stated), where settlement could not be simulated, showed that lobe formation did not appear abrupted (Hüssy, 2008). Interestingly, this was also reported to occur in wild Baltic cod too, from sizes of less than 15 cm and up to 30 cm, suggesting a similar unabrupt increase in the formation of lobes, although this seems to be based on more scarce field observations (Hüssy, 2008). Altogether, this discrepancy between findings in **Paper I-II** (e.g. **Figure 3**) and Hüssy (2008) indicates a plasticity in the otolith shape ontogeny guided by environmental influences (i.e. during/post settlement). The idea that environmental conditions influence more than genetics was further supported by the lack of differences in otolith crenulation between the co-located NC and BS cod juveniles, both before and after settlement although they differed genetically (**Paper II**, see also; Fevolden and Pogson, 1997; Makeenko et al., 2014). This was revealing because, elsewhere, otolith shape has been found to significantly differ between adult NC and BS cod as they generally have contrasting preferences of habitat, i.e. coastal and fjord areas vs. the Barents Sea) (Stransky et al., 2008a; Michalsen et al., 2014). The co-located juveniles, on the other hand, had likely been subjected to the same processes of transportation and dispersal, and thus, experienced similar environmental conditions upon settlement (see **Paper II**).
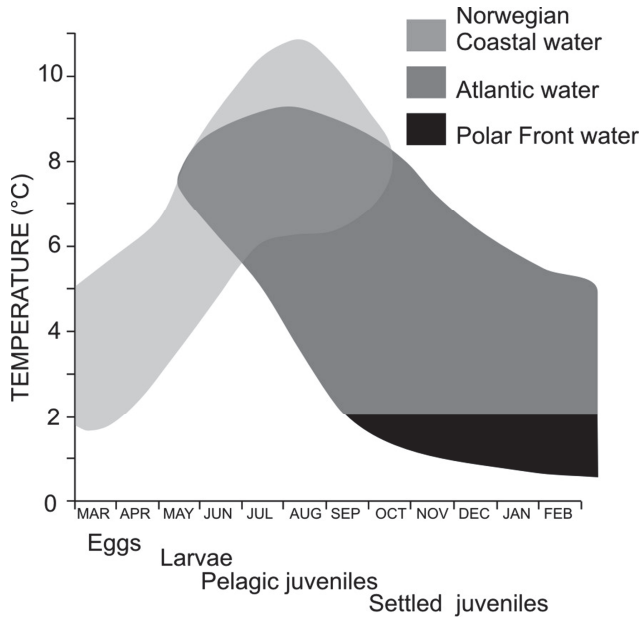
**Figure 5. Ambient temperatures of Barents Sea cod during the first year in life.**
Temperature trajectory with time was presently found to correspond well with otolith lobe
formation during the juvenile stage (see **Figure 3**). Figure from Sundby (2000) (with
permission from Svein Sundby, IMR).

## 4.2 Sexual maturation and spawning

### 4.2.1 Environmental influences during reproduction

Among all cod stocks, spawning zones have, to my knowledge, only been reported in
the BS and NC cod stocks. However, sexual maturation have been linked to
discontinuities or transitions in the otolith zone structure in several other species also,
such as the Atlantic halibut (*Hippoglossus hippoglossus*) (Devold, 1938; Olsen, 1956),
North Sea plaice (Rijnsdorp and Storbeck, 1995) and orange roughy (Francis and Horn,
1997). Additionally, according to Pearson (1996), earlier studies on pike-perch (*Sander*
sp.) and freshwater bream (*Abramis* sp.) have shown that onset of maturity apparently
affects timing of otolith annulus. Other studies have also shown that otolith growth from

the early year(s) in life (being immature) can indicate if the individual will mature early or late in life (e.g. Reglero and Mosegaard, 2006), although this does not directly suggest a otolith transition linked to the age at sexual maturation. Nevertheless, none of these studies have conducted proper validation of the link to onset of maturity, neither in field (e.g. by mark-and recapture studies) or experimentally in the lab. Hence, they either indicate uncertainties around the zone interpretations or uncertainties in the link to maturation, where conclusions are limited to "a probable relationship" between onset of sexual maturation and the otolith marks.

Altogether, there is a limited number of fish species where otolith transitions have been found related to reproduction, relative to the significant number of species where otoliths are studies. This supports the idea that the energetical and physiological changes that fish generally undergo during reproduction are not solely sufficient to cause distinct otolith transitions. It is also reasonable to assume that environmental circumstances related to spawning migrations and reduced feeding before and during spawning is likely to contribute to, if not fully determine, the observed changes in otolith zone formation. This was also indicated by Rollefsen (1933), who pointed at the environmental changes associated with the long-range spawning migration and associated reduced feeding in the BS cod. However, long migrations cannot be argued to apply to the same extent in the more locally spawning NC cod populations, or in other cod stocks for that matter (Bergstad et al., 1987; Brander, 2005). Further, later studies have shown that mature cod also feed at the Lofoten spawning grounds throughout the spawning season (Michalsen et al., 2008).

## 4.2.2 Effects of reproductive investment on otolith zonation

Reproduction in fish species with a r-selection strategy (high fecund species), such as in cod, may require substantial energy reserves (Lambert and Dutil, 2000). This will typically involve trade-offs between competing needs of growth, maintenance and reproduction (Folkvord et al., 2014). Further, the otolith accretion rate is closely linked to the metabolic rate (Mosegaard et al., 1988; Wright, 1991), and otolith opacity (optical density) is positively affected by feeding (Høie et al., 2008). The energy depletion

(Kjesbu et al., 1991) and the changes in endolymph chemistry (Kalish, 1991b) that are associated with the sexual maturation and gonad development, and the reduced appetite during the spawning period (Fordham and Trippel, 1999), may altogether suggest that otolith zone formation could also be affected by reproduction. In essence, one could expect that both opacify and accretion rate decline in years with reproduction. These characteristics are also in compliance with the spawning zones seen in cod otolith (Rollefsen 1933) as they are recognized as narrower annual increments (particularly the opaque zone type) where the translucent zone sometimes become clearer/more distinct.

In **Paper III**, we demonstrated that reproduction *per se* not necessarily affect the otolith zone structure. Otoliths of spawners that invested relatively little energy in gonadal growth (i.e. spawners with low weight loss during spawning) were apparently unaffected. On the other hand, individuals that invested relatively much more energy in reproduction had a significant decline in otolith growth and opacity from autumn to spring, a pattern that differed from the immature fish where otolith growth did not change very much (**Paper III**). This suggests that otolith zonation in principle are affected by either the amount of energy diverted to gonadal growth and gametogenesis, or more simply energy depletion. However, it seemed that this was not always sufficient to induce recognizable spawning zones similar to those reported in wild cod (Rollefsen, 1933; Mjanger et al., 2000). Considering that annual investments in reproduction vary significantly in cod, particularly in the first years of mature age where investments are typically low in the first and third year of reproduction (Trippel et al., 2014), spawning zones may not reliably encompass spawning among all young mature cod (**Paper III**). This could possibly explain why Rollefsen (1933) "only" found spawning zones in about 60% of the otoliths sampled from mature cod at the spawning grounds in Lofoten.

## 4.2.3 Skipped spawning

Although skipped spawning is a common phenomenon in cod (Rideout et al., 2000; Skjæraasen et al., 2012), there are few signs of absent (or disrupted) spawning zones in otoliths of mature cod once they have deposited one of multiple spawning zones (J. A. Godiksen, personal communication, February 05, 2018), based on regular otolith

readings which include identification of spawning zones (Mjanger et al., 2000). This obvious mismatch between spawning zones and actual spawning suggests that other factors than maturation and spawning may induce a "spawning zone". Fish that skip spawning have typically insufficient energy to initiate gamete development in the autumn (Skjæraasen et al., 2012). Considering that maturation has high energy cost and cause nutritional depletion (Kjesbu et al., 1991) negatively affecting otolith growth and otolith opacity (**Paper III**), it is possible that the proximate reasons for skipping also induce these so-called spawning zones. The term spawning zone seems therefore to be imprecise, and should not by any means, be used as direct indicator of spawning, although the use as an indicator of onset of maturity could be more correct.

## 4.3 Endogenous and exogenous influences on otolith formation

In this work I have shown in collaboration with my co-authors that major life history event in cod may cause changes both to the growth structure and outer shape of otoliths. In order to precisely establish the relationship between each event and the observed otolith features, it was necessary to investigate how underlying factors influence otolith formation during each specific life history events. Numerous studies have shown that both otolith growth and shape formation, overall, is determined by both endogenous and exogenous factors, (e.g. Campana and Thorrold, 2001; Capoccioni et al., 2011), but that the relative contributions may change with age (Vignon, 2012).

Although there are gaps in the understanding of the biomineralization of otoliths, this process is indeed linked to other endogenous processes within the fish body. As life history events often involve physiological changes, which often is linked to environmental changes, otoliths have been shown to be useful life history recorders for example based on biochemical signals in the otolith composition (e.g. Kalish, 1991b; Grønkjær, 2016; Loewen et al., 2016). Primarily, the otolith mineralization depends on the chemical properties of the fluid in the endolymphatic sac of the inner ear. This mainly involves regulation of pH (maintaining a high alkalinity), transport and

regulation of ion concentrations, and production of organic matrix and protein components (Gauldie and Nelson, 1990; Wright et al., 2002). These characteristics are again closely linked to other physiological processes in the fish.

Through changes in the properties of blood plasma, and thus the chemistry of the inner ear endolymph, studies have, for example, shown that; hormonal regulations in the endocrine system control the periodicity of micro-increments (Campana and Neilson, 1985), osmotic stress may induce growth checks (Wright et al., 1992), starvation reduce the otolith accretion rate (Payan et al., 1998), and development of gonads change the chemical composition of otoliths (Kalish, 1989; Kalish, 1991a). In terms of otolith growth, studies have further shown that metabolic expression, rather than somatic growth, governs the rate of otolith accretion (Mosegaard et al., 1988; Wright, 1991).

Fablet et al. (2011) elegantly modelled the growth structure of otoliths (i.e. accretion rate and deposit/zone type) in relation to the effects of temperature, feeding levels and fish metabolism in cod, with the aim to explain poorly understood observations in otolith formation. However, a natural next step in this approach would be to explicitly integrate effects from life history events. This would probably involve algorithmic changes that accounts for confounding effects between different factors directly or indirectly influencing the mineralization process, a regime that may change during life history events, and/or gradually throughout life. Vignon (2012) has for example suggested a shift form ontogenetic-driven shape development at early life stages, to more environmentally influenced shape formation in adults.

As a whole, based on findings in **Paper I-III**, and the overall review of the other mentioned studies, I have pointed at the underlying factors that are likely to facilitate (or contribute to) changes in otolith phenotype, and evaluated their contributions to observed otolith features in cod (**Figure 6**). This work has also included how the mineralization is expressed in terms of growth rate, opacity, lobe formation. In **Paper I** we demonstrated that otolith lobe (shape) formation is closely linked to juvenile size, suggesting that this process is mainly ontogenetically driven, perhaps due to a shape-functionality-based selection for sensory abilities during juvenile settlement (e.g.

Gauldie and Crampton, 2002; Cruz and Lombarte, 2004; Lombarte and Cruz, 2007). However, feeding (Hüssy, 2008) and temperature (**paper II)** have also been found to significantly influence on the shape (i.e. lobe formation), indicating that exogenous factors are operational. The findings in **Paper II** further indicate that environmental condition is probably more important than stock genetics in cases where stocks are discriminated by otolith shape.

In **Paper III**, we show experimentally that endogenous factors can play a role in the formation of spawning zones. In cases where energy investments in reproduction were relatively high, a decrease in otolith growth and translucent zone width was found. However, clear spawning zones as they are recognized in otolith of wild cod (Rollefsen, 1933) were not detected, indicating that the physiological changes directly related to maturation and spawning *per se* are not always sufficient to induce a spawning zone. In fact, field studies by Marshall et al. (1998) found that poor growth in immature BS cod generated a reduction in otolith growth, which they suggested could have been interpreted as indicating the onset of maturity. It is therefore likely that indirect factors associated with the spawning migration and/or changes in food intake as such could be of more importance for the formation of the narrow and relatively distinct translucent spawning zones.
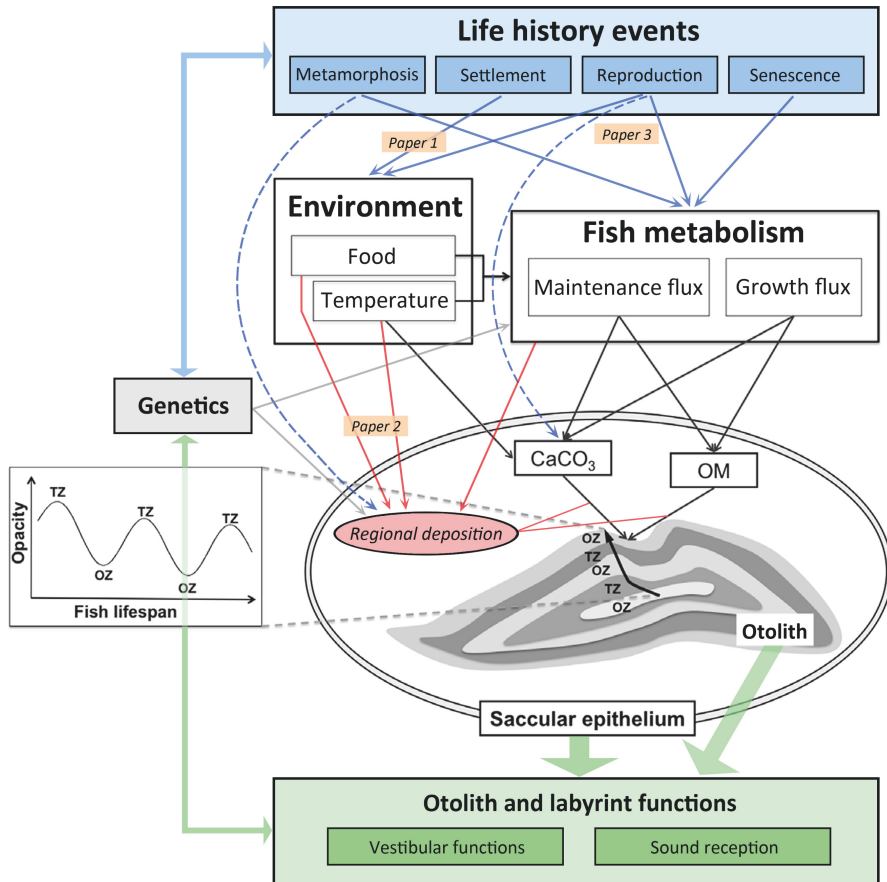
**Figure 6. The key influences from life history events, environment and metabolism on fish otolith growth and shape formation.** Otolith formation is based on the accretion of calcium carbonate ($CaCO_3$) embedded in an organic matrix (OM) in which precursors are synthesized by the saccular epithelium under the influence of the endolymph chemistry (Fablet et al., 2011). Seasonal environmental and physiological variations induce changes in the ratio between $CaCO_3$ and OM resulting in alternated deposition of translucent (TZ) and opaque (OZ) zones, which appear respectively as dark and bright zones under reflected light. The ontogenetic, physiological, behavioural, and environmental changes take place during life history events may influence biomineralization both directly (Kalish, 1991b) and indirectly through changes in feeding and temperature affecting the metabolic rate (Mosegaard et al., 1988; Høie et al., 2008). Both endogenous and exogenous factors were also shown or indicated

to impact otolith formation in cod, both during settlement (**Paper I-II**) and sexual maturation (**Paper III**), in terms of otolith growth rate, opacity and lobe formation. Figure and text are adapted from Fablet et al. (2011) with additional information of key life history events (blue boxes and lines), genetic influence (grey), regional otolith deposition (red), and otolith and labyrinth functions in sensing sound, balance and orientation (green).

## 4.4 Concluding remarks and future perspectives

This work has demonstrated that life history events can affect otoliths in terms of growth rate, macrostructural zone structure, and outer shape. Evaluating the underlying influences in otolith formation is a daunting task involving a complex network of endogenous and exogenous factors that influence the biomineralization process through different pathways (e.g. **Figure 6**). The results in this thesis, in combination with other published literature, suggest that changes found in cod otoliths during settlement (i.e. lobe morphology) and those presumed to be linked to sexual maturation and spawning (i.e. spawning zones) in both cases are determined by a combination of endogenous and exogenous factors. It could, however, not be fully established whether the markedly decline in otolith crenulation (reduction in lobe formation) during settlement was determined by an evolutionary adaptation of shape-based functionality, or an expression of environmental change. Yet, an evaluation of the overall findings suggests that temperature and feeding conditions were likely to have played a major role in the settlement induced otolith shape transformation. Similarly, environmental effects seemed to be important to the formation of the so-called spawning zones that are typically observed in BS and NC cod otoliths. Although reproduction was found to directly influence otoliths in terms of reduced growth and changed zone structure, the effects were reserved to individuals with high reproductive (energy) investments. This suggests that the individual energy level, as a premise for metabolic activity, depending on the natural growth conditions of the individual, acts as a proximate factor in the formation of spawning zones. Since poor feeding and growth conditions are the main causes for fish to skip spawning, while there are clear indications that spawning zones

are deposited also when skipping takes place, calls for a caution in the use of spawning zones as direct indicator of reproduction. It is therefore recommended further investigations on this topic, where perhaps fine scale analyses of otolith macrostructures may reveal differences between skippers and spawners, which presumably are not noticed trough regular age reading. One approach in the field, could be to sample otoliths and gonad tissue from large sized cod that remain in the Barents Sea during the spawning period in Lofoten, and to qualitatively analyse the otolith zone structure combined with determination of current oocyte sizes and maturation stage.

On a more general basis, an interesting and promising approach is the use of computer-assisted interpretation of otoliths (e.g. Fablet and Le Josse, 2005). I believe this will become increasingly important in the years to come, as we already see a rapid development in the fields of "big data" and "machine learning". This would represent an objective, precise and accurate method of extracting age data and other information of life history (or environment). However, such a technological approach will always be limited by the current knowledge we have on how otoliths form. This emphasise the importance with a continued effort in validating otolith characteristics that we assume are linked to a certain periodicity or to specific life history events, and to progress in the work on experimentally establishing precise relationships between underlying factors and the otolith formation, for example through comparative multispecies studies.

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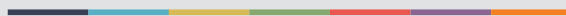
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